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Role of Acetic Acid Bacteria in Food and Beverages

Running title: Role of acetic acid bacteria in food

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SUMMARY

Acetic acid bacteria (AAB) are microorganisms widely distributed in nature. Although this group is involved in the spoilage of some foods, AAB are of great industrial interest, and their functionality is still poorly understood. AAB converts ethanol, sugars, and polyols into various organic acids, aldehydes, and ketones via oxidative fermentation. These metabolites are produced during a succession of biochemical reactions in various fermented foods and beverages, such as vinegar, kombucha, water kefir, lambic beer, and cocoa. Furthermore, important products such as gluconic acid and ascorbic acid precursors can be produced industrially from their metabolism. The development of new AAB-fermented fruit drinks with healthy and functional appeal is an interesting niche for research and the food industry to explore, as it can meet the needs of a wide range of consumers. Exopolysaccharides such as levan and bacterial cellulose (BC) have unique properties, but they need to be produced on a larger scale to expand their applications in this area. This work emphasizes the importance and applications of AAB during the fermentation process of

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various foods, as well as the role of AAB in the development of new beverages and the numerous applications of levan and BC.

Keywords: acetic acid; food; beverage; oxidative fermentation

INTRODUCTION

AAB are mesophilic, gram-negative bacteria that belong to the *Acetobacteraceae* family. They can be single, in pairs, or chains and have an ellipsoidal to elongated shape (rods). Their width varies from 0.4 to 1.0 µm, and their length ranges from 0.8 to 4.5 µm. AAB do not sporulate *(1).*

They show positive catalase and negative oxidase reactions, as well as strictly aerobic metabolism with oxygen as the terminal electron acceptor *(1)*. According to Laureys *et al. (2*), AAB grow well between pH 5.0 and 6.5 but can also grow at pH 3.0 - 4.0 and even lower. The optimum temperature for growth is between 25 and 30 °C, and typically, no growth occurs above 34 °C *(2,3).* However, thermotolerant strains can continue to grow at 37 °C, and some strains can even grow at temperatures as high as 42 °C (*4,5*).

To date, twenty genera have been described in the family *Acetobacteraceae*, among which the ones with the highest number of species are *Acetobacter, Gluconobacter, Asaia, Komagataeibacter, and Gluconacetobacter* (*6,7*). The group can oxidize various types of sugars, sugar alcohols, and alcohols to their respective aldehydes, ketones, and corresponding organic acids through an incomplete oxidation process called “oxidative fermentation”, from which they obtain their energy *(3)*. *Acetobacter* and *Komagataeibacter* spp., for example, are specialized in converting ethanol to acetic acid via two successive oxidative steps and are thus common in alcoholic and acidic environments, such as the vinegar industry (*8,9*). They also present a complete set of citric acid cycle (CAC) enzymes, which are required for the further oxidation of organic acids to CO_2 and H_2O *(3)*. In contrast, *Gluconobacter* spp. occur preferentially in sugary niches and are particularly proficient in the oxidation of sugars and sugar alcohols (*10,11*). Due to a lack of CAC enzymes, *Gluconobacter* species are unable to superoxide acetate to CO_2 and H_2O, but they are useful in the biotechnological synthesis of precursor compounds of vitamin C (L-sorbose), gluconic acid (GA), and its derivatives, dihydroxyacetone, and miglitol (*12,13*).

The bacterium *Gluconacetobacter diazotropicus* is the most well-known member of the genus *Gluconacetobacter*, which plays an important role as a nitrogen-fixing bacteria in plants. In addition, *G. diazotropicus* produces indole-3-acetic acid and gibberellins A1 and A3, which are important hormones that control plant growth (*14,15*).

The genus *Asaia*, on the other hand, has been linked to beverage spoilage and has recently been found to be a symbiotic microorganism in malaria-carrying mosquitos (*16*). In addition, the role of AAB in the production of exopolysaccharides (EPS) is highlighted, the most valuable being bacterial cellulose (BC) and levan, produced mainly by the species of *Komagataeibacter*, *Kozakia*, *Gluconacetobacter*, *Neoasaia* and *Gluconobacter* (*3,8*). AAB are widely distributed in alcoholic, sugary, and acidic environments (*14*). They are often seen only as spoiling agents in wine, where acidity is undesirable, but their role in the production of fermented foods such as vinegar, kombucha, water kefir, lambic beer, and cocoa, as well as in the bioconversion of specific products, such as ascorbic acid, and the applicability and functionality of levan and BC (Fig. 1), is still quite limited. Therefore, the objective of this review is to demonstrate the many advantages of AAB in this area, also encouraging their research in other application areas.

<Fig. 1>

AAB IN FOOD AND BEVERAGE FERMENTATIONS

Vinegar

Vinegar production has been around for over 10,000 years *(3)*. Despite not being considered a “food” and not having a high nutritional value, vinegar is consumed by people of all social classes all over the world, and it differs in terms of the raw materials used, manufacturing technologies, and its wide range of applications (Fig. 1a) (*3,17*).

The definition and standards of vinegar identity and quality have some local differences, but in general, food regulatory agencies consider vinegar to be the result of a double fermentation (first alcoholic, then acetic) of sugary substrates (*18*). In Brazil, the MAPA (Ministry of Agriculture, Livestock and Supply) defines acetic fermented as a product with a minimum volatile acidity of 4 % (g/100 mL, expressed in acetic acid) obtained from acetic fermentation of alcoholic fermented of fruit, cereal, other vegetables, honey, vegetable mixture, or hydroalcoholic mixture. The acetic fermented product can be called “vinegar of...”, plus the name of the substrate used (*19*).

The substrate used in the processing of vinegar is mostly of plant origin, including fruits (*e.g.,* vinegar of grapes, cereals, onion, cider, apple, mango, *etc.*), except for vinegar of honey and whey (*18,20*). The chemical composition of the raw material has a strong influence on the selection of microorganisms and determines the dominant species involved in the acetification process (*21*). Table 1 shows the main AAB species involved in vinegar production (*1,7,22-31*).

Generally, vinegar is made through two fermentation processes: alcoholic fermentation and acetic fermentation (*61*). Under anaerobic conditions, yeasts (typically strains of *S. cerevisiae*) convert

fermentable sugars to ethanol, whereas in acetic fermentation, AAB convert ethanol to acetic acid by the activity of two membrane-bound enzymes located on the outer surface of the cytoplasmic membrane (periplasmic side) (*3,18*). First, alcohol dehydrogenase (ADH) oxidizes ethanol to acetaldehyde, which is then oxidized to acetic acid by aldehyde dehydrogenase (ALDH) (*61*). On the other hand, some rice and cereal vinegar made from starchy raw materials include a distinct saccharification step prior to alcoholic fermentation (*62*).

Three main methods can be used in industrial vinegar production: slow, traditional Orleans or French (surface acetification carried out in wooden barrels), fast Generador (production conducted under forced aeration with wood chips or other inert material), and rapid Submerged (modern or industrial; batch acetification with forced aeration and agitation) (*18,63*). In the production of traditional vinegar, the acetification is typically made using a culture from a previous batch known as "seed-vinegar" or "mother of vinegar", whereas selected cultures are added to ensure large-scale vinegar production, higher yield, safety, process stability, shorter fermentation time and product losses, as well as avoiding undesirable characteristics caused by uncontrolled fermentation (*26,64*). The use of specific AAB starters, however, is still far from being a common practice (*26*).

The microbiota that leads to vinegar production is complex and includes several genera of AAB; however, *Acetobacter* and *Komagataeibacter* species have a strong capacity to produce acetic acid, and both genera also exhibit high resistance to high ethanol and acetic acid concentrations, which are essential characteristics required for industrial vinegar production (*3,65*). Thermotolerant AAB have also been introduced for the production of a variety of valuable products, including vinegar (*50*). They are advantageous for industrial vinegar fermentation because they allow for stable fermentation with lower cooling costs, particularly in tropical countries (*66,67*).

Vinegars have a wide range of applications. Vinegars are frequently used as preservatives, flavoring agents, and as ingredients in mayonnaise, salad dressings, mustard, and other condiments (*17,20,68*). Its use as a routine medicine for humans and animals dates back to remote antiquity; in addition, it can be used as a cleaning agent and in some countries even as a healthy drink (*3,17*).

Although vinegar is traditionally used as a flavoring and food preservative, recent scientific studies have reported that regular consumption of vinegar can promote beneficial physiological health effects (*3,65,69*). Among the therapeutic properties presented by vinegar are its antibacterial activity, regulation of blood pressure and glycemia, antioxidant activity, prevention of cardiovascular diseases, and prevention of obesity (*8,70*). In addition to acetic acid, some vinegars contain several bioactive compounds, such as polyphenols, that contribute to their taste, smell, and specific functions. Considering that different vinegars can be produced from different raw materials, processes, and

species of AAB, understanding the relationship between the compounds present and the functionality of vinegar is of great importance (*20,70*).

<Table 1>

Kombucha

Kombucha is a popular drink usually consumed in Asia (*35*) (Fig. 1b). It is characterized by being a nonalcoholic beverage, refreshing, with accentuated acidity and a specific flavor (*71*). Traditionally, it is made by fermenting sweetened tea, but other plants (*e.g*., cereals or plant leaves) or animal (*e.g.,* milk) raw materials, as well as mushrooms, can also be used (*72*). Fermentation lasts approximately 7 to 10 days and occurs quickly after adding the cellulosic layer called tea fungus or SCOBY (Symbiotic Colony of Bacteria and Yeast) to the sweetened tea (*73*). The microbial composition of kombucha varies significantly from batch to batch depending on its origin, substrate, and fermentation conditions (*74*) It is predominantly composed of AAB, which include *Komagataeibacter and Gluconobacter,* and *Acetobacter* species are less abundant (*71*). *K. xylinus* is considered one of the most important species involved in the fermentation of kombucha due to its superior capacity for cellulose synthesis (*37*). Table 1 shows the main AAB species involved in Kombucha fermentation (*32–37*).

In addition to AAB, a wide range of yeast species can be found in the kombucha, including species of the genera *Zygosaccharomyces*, *Candida*, *Kloeckera/Hanseniaspora*, *Torulaspora, Pichia, Brettanomyces/Dekkera, Saccharomyces, Lachancea, Saccharomycoides, Schizosaccharomyces*, and *Kluyveromyces* (*34,75*). Lactic acid bacteria (LAB), such as *Lactobacillus, Lactococcus,* and *Bifidobacterium* species, can occur (*75*); however, they do not seem to be a crucial part of the kombucha microbial ecosystem since they are not always present (*2*).

In this symbiotic relationship, the yeast community hydrolyses sucrose present in the medium to glucose and fructose and produces ethanol from glucose. AAB use glucose, fructose and ethanol to produce gluconic acid, glucuronic acid, acetic acid, D-saccharic acid-1,4-lactone, and BC (*37,71*). The acetic acid produced further stimulates the production of ethanol by the yeasts, and this ethanol is then converted to acetic acid by AAB. The continuous accumulation of ethanol and acetic acid in the medium prevents contamination by various pathogenic microorganisms (*73*).

The composition of kombucha also includes vitamins, phenolic compounds, amino acids, and some hydrolytic enzymes (*35,75*). The chemical profile of Kombucha may be responsible for its multiple health benefits when associated with regular consumption of the drink (*35*). Recently, tea has attracted the attention of researchers and consumers due to its in vitro biological activities, such as antimicrobial activity, antioxidant and anti-inflammatory activity, and anticarcinogenic potential.

However, more clinical investigations and in vivo evaluations should be carried out to confirm the health benefits of the beverage (*75,76*).

Water kefir

Water kefir is a sparkling, refreshing, low-alcohol drink with acidic and fruity flavors (*71*) (Fig. 1c). Its obtainment is given by the spontaneous fermentation of sugar solution, dried fruits, and water kefir grains (insoluble dextran). These translucent grains, which resemble a cauliflower in shape, contain microorganisms that act as an inoculum for the fermentation process (*77*).

The microbial composition of the grains consists of yeasts, LAB, and AAB, with the bacterial community presenting a higher diversity. Some of the main microorganisms of water kefir are LAB, such as *Lentilactobacillus hilgardii*, *Liquorilactobacillus nagelii*, *Lacticaseibacillus paracasei*, and *Bifidobacterium aquikefiri*, and yeasts, such as *S. cerevisiae* and *Dekkera bruxellensis* (*39,40*). During the first 24 h of fermentation, yeasts (mainly *Saccharomyces cerevisiae*) consume sucrose producing alcohol. Furthermore, yeasts hydrolyze sucrose by the action of invertase, promoting an increase in glucose and fructose, which are then metabolized by LAB and AAB (*3,39*). In the advanced stages, ethanol concentrations decrease due to oxidation of ethanol to acetic acid by AAB (*e.g., Gluconobacter*, *Komagataeibacter,* and *Acetobacter*) (*40*). Table 1 shows the main AAB species involved in water kefir fermentation (*38–40*).

At the end of fermentation, the main products are ethanol, lactic acid, acetic acid and other metabolites, such as mannitol, glycerol, esters, aldehydes, and other organic acids (*78,79*). Kefir drinks, such as Kombucha, have been linked to numerous health benefits. The beverage is well known for having potentially “probiotic” and antimicrobial properties against a wide range of pathogenic bacteria (*78,80*). Furthermore, studies have shown that water kefir has antihyperlipidemic properties (*81*), antioxidant activity (*39,82*), anticarcinogenic activity, hepatoprotective effects, anti-inflammatory effects, and gastroprotective effects, among others (*79*). Due to the numerous positive effects of kefir, several substrates have been investigated for the adaptation of its grains (*39,82–84*). This has enabled the emergence of new functional drinks with characteristics similar to those of the traditional brown sugar kefir (*78*).

Lambic beer

Lambic beer, originally from Belgium, is probably one of the oldest beer styles brewed to date (*85,86*) (Fig. 1d). It is a refreshing, alcoholic, acidic beer with fruity notes and only a few residual

carbohydrates. The spontaneous fermentation process occurs in the presence of water, barley malt, unmalted wheat, and aged dry hops, and maturation takes up to three years in wooden barrels (*71*).

An in-depth examination of the microbial dominance pattern over three years of lambic beer fermentation revealed four distinct phases (*21*). Table 1 shows the main AAB species involved in lambic beer fermentation (*41–43*). The first phase (from the start up to 1 month of fermentation) begins with members of the *Enterobacteriaceae* family, which are inhibited by ethanol accumulation produced by wild (oxidative) yeast, acidification by enterobacteria and AAB (*A. orientalis)*, and glucose reduction by microbial growth in general (*71,87*). *Gluconobacter* species such as *G. cerevisiae* have also been isolated during this phase, probably as a result of the combination of a monosaccharide-rich environment and low ethanol concentrations (*42*).

The second phase of ethanol fermentation, referred to as the most important, extends until the fourth month, with yeasts (*Saccharomyces cerevisiae*, *S. bayanus/pastorianus and S. uvarum*) being the main representatives for the conversion of carbohydrates into ethanol and carbon dioxide (*88*). After 4 to 10 months of fermentation, the acidification phase (third phase) takes place. This phase is characterized by the predominance of the LAB and AAB species, which together produce lactic acid and acetic acid, resulting in a pH drop below 3.5 (*41,87*). During this fermentation stage, the most frequently isolated LAB species are homofermentative *Pediococcus damnosus* and heterofermentative *Lactobacillus brevis*, whereas the most frequently reported AAB species are *A. pasteurianus* and *A. lambici.* LAB species produce both lactic and acetic acid from saccharides, while AAB species oxidize ethanol to acetic acid and produce acetoin from the lactic acid produced by LAB species (*41,89*).

After the acidification phase, the final or maturation phase begins and can last for several years (*89*). LAB, AAB, and primarily *Brettanomyces* yeast species are present during this phase. The LAB and AAB species that proliferate during this phase are typically the same species that are present in the previous phase (*41*). *B. bruxellensis* and other species belonging to the genus *Brettanomyces* play a key role in the final flavor formation of lambic beer (*90*) since they synthesize precursor compounds responsible for the characteristic Brett flavor (volatile phenolic compounds 4-vinylguaiacol and 4-vinylphenol) of lambic beers and several ethyl esters, such as ethyl acetate and ethyl lactate. Together with *Brettanomyces,* AAB may also participate in ethyl acetate formation (*43*).

AAB are abundant during major periods of traditional lambic beer production's first fermentation year, producing much larger concentrations of acetic acid and acetoin (from in the liquid/air interphase of the casks). The formation of acetic acid by AAB and the subsequent formation of ethyl acetate are desired compounds for complex lambic beers; however, excessive AAB development must be controlled to avoid an unfavorable flavor profile (*42,87*).

Cocoa

Cocoa bean (*Theobroma cacao* L.) is the main raw material for the manufacture of chocolate (*91*) (Fig. 1e). Once harvested from freshly harvested cocoa pods, raw cocoa beans are subjected to a complex fermentation that involves physical and biochemical transformations in all bean structures and lasts 3–7 days depending on factors, including the seed genetic origin, agro-ecological conditions, and the method used (*92,93*). This process is primarily regulated by yeast, LAB, AAB, and *Bacillaceae* (particularly *Bacillus*) that use the cocoa bean pulp as a growing substrate. Several molecules are released during microbial fermentation of cocoa, giving chocolate its distinctive aromatic profile, reducing bitterness and astringency, and finally killing the embryo to prevent its germination (*94*).

During the fermentation of cocoa beans, three main stages can be identified (*94*). Yeasts are the most prevalent microorganisms in the first 24 hours of fermentation, converting pulp sugars to ethanol and carbon dioxide via alcoholic fermentation (anaerobiosis) (*45*). They are involved in the production of pectinolytic enzymes, which degrade pectin and allow oxygen to enter the cocoa pulp (*93*). Furthermore, yeasts produce a large number of aroma compound precursors that significantly contribute to the development of the chocolate aroma profile (*47*). Alternatively, in parallel with yeast, fructophilic LAB species use fructose as an energy source, with or without citric acid conversion, and heterofermentative LAB species grow by converting glucose to lactic acid, acetic acid, ethanol, carbon dioxide, and/or mannitol (*95*).

The second stage is distinguished by an increase in lactic acid concentrations as a result of an increase in LAB populations and a reduction in yeasts (*94*). Lactic acid produced in seeds is important to activate endogenous enzymes and contribute to the generation of chocolate flavor and aroma (*45*).

During the third phase, the high ethanol concentrations (metabolized by yeast) and oxygen ingress because of pulp liquefaction provide conditions for the growth of AAB (*44*). Table 1 shows the main AAB species involved in cocoa bean fermentation (*44–48*). Ethanol, which is the main energy source, is converted into acetic acid by AAB, particularly *Acetobacter* species, while lactic acid produced by LAB serves as the primary carbon source (*95*). Lactic acid is primarily oxidized into acetoin and, to a lesser extent, acetic acid due to low pyruvate decarboxylase activity in *Acetobacter* (*95*). The entry of acetic acid and ethanol, along with the temperature increase (approximately 50 °C), causes the death of the seed embryo and induces a series of endogenous reactions that produce flavor, aroma, and color precursors to the chocolate raw material (*47,96*). As a result, the counts of yeast, LAB, and AAB decline, favoring the growth of *Bacillus* spores in later stages of cocoa bean fermentation (*94,95*).

Among the different genera of AAB, *Acetobacter* is the most common during cocoa fermentation (*45*). It includes *A. ghanensis* and *A. senegalensis,* which predominate mainly at the beginning of fermentation, whereas *A. pasteurianus* and occasionally *Acetobacter lovaniensis, Acetobacter syzygii*, or *Acetobacter tropicalis* prevail during the last phase, when the concentration of ethanol is high (*45,95*). *A. pasteurianus* prevails during the fermentation of cocoa due to its ability to oxidize ethanol, lactic acid, and mannitol, as well as its tolerance to acidity and heat (*95*). On the other hand, *Gluconobacter* species can be prevalent at the beginning of the fermentation process due to their preference for sugar metabolism. However, their growth is undesirable, as this can result in the production of gluconic acid from glucose and off-flavors, impacting the final quality of cocoa beans (*45*).

OTHER METABOLITES PRODUCED BY AAB

AAB can participate as biocatalysts for the industrial manufacturing of a wide range of compounds, in addition to being employed commercially in the manufacturing of vinegars and other fermented foods (*8,14*) (Fig. 1f). *Gluconobacter* strains, in particular *G. oxydans*, can carry out oxidative fermentation of sugars and sugar alcohols, resulting in the formation of L-sorbose, ketogluconic acids, dihydroxyacetone (DHA), and cyclic ketones, among other compounds (*21,50*). The oxidative fermentation of L-sorbose from D-sorbitol is the most classic example observed during the production of vitamin C by *Gluconobacter*. Other precursor intermediates, such as 2-keto-D-gluconic acid (2KGA) from GA, 2,5-diketo-D-gluconic acid (25DKGA), and 5-keto-D-gluconic acid (5KGA), are also present in the synthesis route (*14,21*). 5KGA has potential applications for the synthesis of tartaric acid and xylaric acid, in addition to being a precursor for the manufacture of aromatic compounds such as 4-hydroxy-5-methyl-2,3-dihydrofuranone-3, a valuable product used in the food industry (*97*). The microbial production of DHA from glycerol has been explored in the pharmaceutical industry, and it can be used as a tanning agent and as an intermediate for the synthesis of various chemicals and surfactants (*14,98*). *Gluconobacter* species can also be applied in the biotransformation of miglitol precursors, a drug used for the treatment of type II diabetes; in the production of GA, considered a multifunctional acid in the food, feed, beverage, textile, pharmaceutical, and construction industries; and in the manufacture of shikimic acid, a key intermediate for numerous antibiotics (*8,12,49,50*) (Table 1).

DEVELOPMENT OF NEW PRODUCTS FROM AAB

Currently, consumers have shown a growing interest in foods that, in addition to satisfying their hunger, can also prevent nutrition-related diseases and improve mental health (*99*). According

to the Food and Agriculture Organization of the United Nations (FAO), fruits constitute an important part of a healthy diet. In addition to being a source of dietary fiber, vitamins, minerals, and beneficial phytochemicals, fruits may help lower risk factors for diseases such as overweight/obesity, chronic inflammation, high blood pressure, and high cholesterol (*100).*

Fruit-based fermentation has improved the nutritional and functional quality of beverages. In addition, rising consumer demand for lactose-free products with low fat content and few additives make this type of fermentation a promising tool for meeting the needs of obese people with cardiovascular diseases, allergies, intolerances, vegans, and vegetarians (*101–103*).

The development of fruit drinks containing probiotic bacteria stands out among current research (*104–106*). These microorganisms improve mineral bioavailability, digestibility, and organoleptic properties, such as color, flavor, and aroma, in addition to providing a functional beverage (*103*). However, the acidic environment, as well as the presence of anti-nutritional and inhibitory factors in fruits, make maintaining bacterial viability and stability during processing and storage a major challenge (*102*). Given this, the fermentation of fruit drinks with AAB becomes a viable alternative, since they can oxidize a wide range of substrates and are typically found in sugary and high-acid environments (Table 1).

Fruit vinegar drinks, for instance, are gaining popularity in North America (Fig. 1g). By definition, the product must be made from at least one type of fruit and contain at least 300 g of fruit juice for each liter of fermented product. These beverages have been categorized according to the concentration of acetic acid as low acidity (< 3 % v/v) and high acidity (5 - 7 % v/v) (*107*). Furthermore, the fermentation method used and the concentration of acetic acid may affect the content of total sugars and soluble solids, titratable acidity, and density (*107*). Regarding its benefits, in vivo animal studies have shown that tomato vinegar drinks can prevent visceral obesity and insulin resistance (*51*), while pomegranate vinegar drinks have been shown to reduce visceral adipose tissue in humans (*108*). Other research suggests that fruit vinegar drinks such as cranberry, blueberry, and tomato could be used to treat hypertension and hypercholesterolemia (*107*). However, according to Chang *et al.* (*109*), continuous consumption of vinegar drinks should be avoided to prevent gastrointestinal injuries.

Another recent approach has been focused on GA fermentation. Although works related to this type of fermentation are still scarce, their results are very promising. The gluconic fermentation of strawberry drink by *G. japonicus* converts glucose into GA while keeping the fructose naturally present in the fruit as a sweetener. This allows diabetics to consume a drink that keeps phenolic compounds (nonanthocyanins) and antioxidant activity practically unchanged (*110*). Furthermore, its composition remains stable for 15 days at room temperature (27−30 °C) and up to 30 days when

refrigerated (4 °C) (*53*). In another study, Hornedo-Ortega *et al*. (*111*) compared the antioxidant activity and anthocyanin composition of alcoholic and gluconic fermented strawberry drinks. The authors concluded that the gluconic fermentation of strawberry beverages by *G. japonicus* is a novel process that preserves the anthocyanin composition and shows higher antioxidant activity values than alcoholic fermentation (*111*). Ordoñez *et al.* (*112*) also demonstrated the safety of strawberry gluconic fermented by demonstrating that none of the eight biogenic amines studied were detected. In addition to the bioactive compounds found in fruits, GA and its derivatives have been shown to have prebiotic properties. This acid promotes the growth of *Lactobacillus* sp. and *Bifidobacterium adolescentis* in the human colon and alters the intestine's metabolic profile (*113*). GA and its derivatives are approved for use in food and are commonly used to preserve and/or improve the sensory properties of dairy products and soft drinks (*113*). The presence of higher proportions of GA in Kombucha, for example, improved the taste of the drink in a study conducted by Li *et al.* (*114*). GA contributes to the pleasantly sour taste, while the acetic acid formed produces an acidic and astringent off-flavor (*114*).

EXOPOLYSACCHARIDES PRODUCED BY AAB

Microbial polysaccharides are produced by a wide range of bacteria, presenting extreme diversity in terms of chemical structure and composition (*115*). AAB, for example, can produce large amounts of EPS, including both homopolysaccharides such as levan and BC and heteropolysaccharides such as acetan or xylinan and gluconacetan (*116–118*). Due to the importance of levan and BC (Fig. 1h) in research and industrial applications, some of their characteristics and main applications in the food industry are discussed in this paper.

Levan

Levan is a polymer composed of D-fructofuranosyl residues joined by β-(2,6) bonds in the main chain and β-(2,1) bonds in the side chain, in addition to having a D-glucopyranosyl residue at the end of the main chain (*119*). Fig. 2 shows the structure of the levan. Levan is commonly biosynthesized by a restricted number of plants in nature, but it can also be produced by several microorganisms, including Archaea, fungi, and a wide range of bacteria (*58,120*). Among the AAB, species of the genera *Acetobacter, Gluconobacter, Gluconacetobacter, Kozakia, Komagataeibacter, Tanticharoenia,* and *Neoasaia* are also capable of producing it (*54–58*) (Table 1).

<Fig. 2>

The synthesis and polymerization of levan occur in the extracellular matrix by the action of the enzyme levansucrase, whose main function is to transfer fructose residues from sucrose by transfructosylation reactions (*121*). The enzyme has high specificity for sucrose and lower activity for

fructose, mannose, raffinose, mannitol, *etc.* On the other hand, inhibition is observed in the presence of glucose and other sugars that have a configuration similar to glucose, such as lactose, galactose, and maltose, as well as other sugar alcohols (*121,122*).

In general, the structure of levans produced by different organisms is similar but differs in terms of molecular mass, degrees of polymerization (DP) and branching (*122,123*). Plant levans have a lower molecular mass and DP than bacteria. Plant levans have a molecular mass of 2000 to 33000 Da and a DP < 100, whereas bacterial levans have multiple ramifications (2 % to 12 %) and a molecular mass of 2 to 100 million Daltons (Da) with DP >100 (*121,123,124*).

In comparison to polysaccharides formed by pyranose rings, the structural characteristic of levan, in the form of furanose rings, plays an important role in the conformation of molecules in solution, providing additional flexibility. Furthermore, the semiflexible chain of the rings interacts intramolecularly and intermolecularly, resulting in a densely packed spherical structure and low viscosity aqueous solutions (room temperature) at concentrations where other polysaccharides would form pastes or gels (*121,122,124–126*).

Xu *et al.* (*127*) observed that aqueous solutions of levan (*Brenneria* sp. EniD312) exhibit Newtonian fluid behavior at low concentrations (3 %; *m*/*V*) and non-Newtonian fluid (pseudoplastic fluid) behavior at high concentrations (6, 9 and 12 %; *m*/*V*) when studying the rheological properties of levan. Levan solutions derived from *Zymomonas mobilis* and *Erwinia herbicola* showed similar results (*128*). At concentrations between 1 and 8 %, however, the behavior of *Bacillus subtilis* levan solutions was completely Newtonian (*128*). According to Xu *et al.* (*127*), levan could be a good additive in the food industry, since its non-Newtonian behavior is interesting for the manufacture of dairy products, syrups, and salad dressings.

Levan solutions are also characterized by exhibiting an atypical behavior when compared to other polysaccharides, in which gel formation is not observed (*129,130*). However, Jakob *et al.* (*131*), when establishing the structure/function relationship of isolated AAB levans, suggested that in solution, increasing their molecular weight reinforces intramolecular interactions to achieve a more compact structure characteristic of a “microgel” with hydrocolloid properties. The authors also reinforce that levans produced by AAB may thus offer new possibilities for applications in food.

Unlike many other polymers, levan does not swell in water, but it has a high solubility in hot water, a variable solubility in cold water, and is insoluble in most organic solvents, with the exception of dimethyl sulfoxide (DMSO). The high solubility of levan in water is mainly attributed to its β-(2,6) bond rather than to the β-(2,1) bond, and the ramifications could only be a supporting factor (*121,122,126*). Levans are nonreducing agents that are not hydrolyzed by yeast invertases or amylases, but they are susceptible to acid hydrolysis (*122*). It decomposes at approximately 225 °C,

and the glass transition temperature is 141 °C (*126*). Another important property of levan is its adhesive strength. Although sugars are characterized by stickiness, the adhesive strength of levan is significantly higher than that of other natural polymers. The branches contribute to its cohesive strength, and the ability to form adhesive bonds with a wide range of substrates is given to its large number of hydroxyl groups. Levan is commonly referred to as a "green" adhesive because it is water-removable and has high-value applications in several areas (*8,121,125*).

In the food area, several studies have explored the effects of levan type-fructooligosaccharides (L-FOS) and levan as prebiotics on probiotic bacteria and the complex gut microbiota; however, there is no conclusive evidence from human trials (*132–136*) (Fig. 3). In animal models, for instance, levan supplementation increased *Lactobacillus* and *Bifidobacteria* viability while inhibiting *Escherichia coli* and *Clostridium perfringens* (*136,137*). Adamberg *et al.* (*132*), using the human fecal microbiota, reported that levan alters the composition of the fecal microbiota and the profile of metabolites, making it a potential candidate for prebiotics. Using metagenomic sequencing to assess the prebiotic activity of levan, Cheng (*138*) also verified alterations in the intestinal microbiota of mice and the stimulation of the production of short-chain fatty acids.

<Fig. 3>

In bakery, EPS are known to improve the rheological properties of dough and the texture, nutritional value, shelf life, and machinability of wheat, rye and gluten-free breads (*56*). Jakob *et al.* (*139*) evaluated the functional effects of different AAB levans (*G. frateurii* TMW 2767, *G. cerinus* DSM 9533, *N. chiangmaiensis* NBRC 101099, and *K. baliensis* DSM 14400) added to wheat-based breads. The addition of two doses of EPS (1 and 2 % *m*/*m* flour) resulted in an increase in volume, a noticeable softening of the fresh breads, and a delay in hardening of the breads after a week of storage. Although LAB and yeasts are common microorganisms in sourdoughs (*54*), Hermann *et al.* (*56*) reported that AAB, such as *N. chiangmaiensis* NBRC 101099 and *K. baliensis* DSM 14400, can grow on a variety of flours (wheat, whole wheat, spelled, and rye) and produce large amounts of levan. Later, gluten-free breads were made with buckwheat and molasses dough fermented by *G. albidus* TMW 2.1191 and *K. baliensis* NBRC 16680, and their volume, crumb hardness, and sensory characteristics were evaluated (*54*). Breads made from the dough had better sensory and quality characteristics, such as higher specific volume and lower crumb hardness. However, the authors pointed out that strong acidification during fermentation could become a challenge in large-scale production (*54*).

Other advantages of applying levan in foods include its use as a fat substitute. Fructans have fat-like properties that improve the flavor and spreadability of dairy products. Furthermore, high molecular weight levans are rarely detected by taste sensors, and odor detection is almost imperceptible due to their low volatility (*120*). Its low viscosity and high solubility make it an excellent

substitute for gum arabic, as the latter also has excellent stabilizing and emulsifying properties for food applications (*122*). In the food packaging industry, levan as a component in edible starch films increased its barrier and mechanical properties in addition to being a cost-effective alternative (*119*). Gan *et al.* (*140*) also developed levan/pullulan/chitosan edible films enriched with ε-polylysine and applied them to strawberry. As a result, they demonstrated that films could help preserve strawberry postharvest quality by minimizing water loss, inhibiting microbial development, and decreasing the respiration rate during storage.

Although this study is not focused on biomedical or cosmetic applications of levan, this EPS has shown several bioactive properties, including antitumor, antimicrobial, anti-inflammatory, hypocholesterolemic, antidiabetic, and immunostimulating activities (*120,121*). As a result, in addition to being a useful EPS for food production, its consumption alone or in food can provide several health benefits to the host.

Bacterial cellulose

BC is a linear glucan composed of several glucose monomers linked by β-(1–4) bonds (*8*) (Fig. 4). This biopolymer can be synthesized by various microorganisms, such as algae and fungi, as well as by various bacteria, including *Achromobacter, Alcaligenes*, *Aerobacter, Agrobacterium, Azotobacter, Gluconacetobacter, Pseudomonas, Rhizobium, Sarcina, Dickeya,* and *Rhodobacter* (*141,142*). Among these bacteria, *Komagataeibacter* species (AAB) (Table 1) (*24,59,60*) are frequently utilized in research and commercial production and are employed as model strains because of their high productivity and ability to metabolize a wide range of carbon/nitrogen sources (*60*).

<Fig. 4>

When cultivated under controlled conditions, *Komagataeibacter* produces highly porous BC structures in the form of pellicules (static culture) or as fibrous suspensions, pellets, spheres or irregular masses (agitated culture) (*142,143*). The synthesis of BC from glucose involves several individual enzymes, catalytic complexes, and regulatory proteins. Briefly, β-glucan chains are formed first, followed by the assembly and crystallization of cellulose chains. In this final stage, the cellulose chains are released from the cell and self-assemble into fibrils (*144*). When compared to plant cellulose, BC has a great number of unique physicochemical and mechanical properties, including higher crystallinity, degree of polymerization, water absorbing and holding capacity, tensile strength, and biological adaptability (*60*). Moreover, plant-derived cellulose is usually incorporated with hemicellulose and lignin, necessitating harsh chemical treatments to remove these impurities (*145*). BC generated by microbial fermentation, on the other hand, has a greater purity and requires less energy and chemical processing for purification (*145*). As a result, BC has been used in a variety of

food-related applications (Fig. 5) since it is a dietary fiber that has been approved as "generally recognized as safe" (GRAS) food by the US Food and Drug Administration (FDA) (*146*).

<Fig. 5>

The "nata de coco", a traditional food consumed in the Philippines and other Southeast Asian countries, is one of BC's most well-known industrial applications. In its manufacturing process, BC is synthesized by fermenting coconut water and then cleaning, washing, chopping, and immersing it in sugar syrup to serve as a dessert (*142,145,147*). A variety of nata-like products have been developed to meet consumer demands. To change the color and flavor of the dessert, different fruit juices, syrups, and other ingredients have been employed. Other items containing nata de coco, such as fruit-flavored pudding, drinks, and jellies, have been marketed all over the world.

In other food systems, BC has also shown promise as a stabilizer, noncaloric bulking agent, and texture modifier. After heat sterilization, the use of an aqueous suspension of BC in liquids such as chocolate drinks prevent cocoa precipitation and stabilizes the dispersion (*148*). In pasty condiments, BC reduces the stickiness and controls the syneresis during storage (*148*). Furthermore, BC promotes firmness in solid foods such as tofu, while it changes the texture of kamaboko by increasing hardness and fraturability (*148*). The addition of BC to meat products such as hamburger and sausage can also reduce fat content without compromising tenderness and juiciness, as well as produce stable emulsions, respectively (*148*).

Following the example of earlier products that were lower in calories, Guo *et al.* (*149*) demonstrated that adding BC/soy protein isolate blends to ice cream as a cream substitute can result in ice creams with low calories, melt resistance, and good texture properties. Surimi products (*150*), cheese (*151*), meatballs (*152*), pork Frankfurters (*153*), and mayonnaise (*154*) are among the other applications of BC as a fat replacer. These findings suggest that BC could be widely used as a food additive in processed foods to improve their quality and shelf life while also lowering the calories in the final products.

BC has also been used as a vegetarian meat preparation when combined with Monascus extract obtained from a naturally red pigmented mold (*155*). The product has a natural meat flavor and is resistant to color and morphological changes. Furthermore, because of its nonanimal origin, this ingredient may be a suitable substitute for animal-based products for some dietary restrictions (*60,142*).

BC has attracted interest in research related to the immobilization of enzymes, cells, and probiotics for use in food. Because of its superior characteristics concerning plant cellulose, BC has provided stability to enzymes against temperature and pH variations (*156*). When compared to free laccase, laccase immobilized on magnetically modified BC showed superior thermal stability at 70 °C

and maintained 65 % of its initial activity after 8 cycles of use (*157*). Similarly, Chen *et al.* (*158*) obtained a retention of 69 % of the original activity after seven recyclings when immobilizing fungal laccase on natural BC.

BC has also been explored as a carrier for cell immobilization, primarily for yeasts in the winemaking process. This approach reduces inoculum preparation costs, as the yeast can be recovered and separated at the end of the fermentation process (*145*). BC has been shown to protect wine yeast from adverse conditions such as high osmotic pressure and low pH (*159*). As a result, the growth of immobilized yeast was better than that of free yeast (*159*). Furthermore, the metabolic activities of immobilized yeast in BC were reported to be higher than those of free yeast (*160*). Immobilized yeast in BC was also shown to have no negative impact on the sensory quality of the final product during repeated batch fermentation (*161*) and can increase the amount of alcohol produced compared to free cells (*162*).

BC has been proven in studies to be an effective matrix for the immobilization of probiotic bacteria (*163*). In this context, Fijałkowski *et al.* (*164*) showed that BC as an immobilization support improves probiotic viability, protecting against adverse conditions of the gastrointestinal tract (*164*). Furthermore, the authors established that the immobilization efficiency depends on the cellulose form, its synthesis method, and the immobilization method (*164*). Similarly, Phromthep and Leenanon (*165*) demonstrated that the BC produced from fruit juice residues and coconut milk resulted in improved survival of immobilized *Lactobacillus plantarum* compared with free cells. Under prolonged incubation, Zywicka *et al.* (*166*) used the BC pellicle as a support for immobilization during prolonged incubation and reported that the cell viability of *L. delbrueckii* was affected after 72 hours. On the other hand, the viability of *L. acidophilus* 016 immobilized in BC Nano Fiber was found to be 71 % for up to 24 days when stored at ambient temperature (35 °C) (*163*). These findings show potential because one of the requirements for a microorganism to be administered for therapeutic purposes is that it remains viable in the food that will be consumed (*164*).

More recently, BC has been reported as a matrix for probiotic films (*167,168*). The films can be used as coatings or wrapped over a variety of foods, providing consumer health benefits, as well as potentially inhibiting the growth of spoilage bacteria and fungi on food surfaces, thus extending the shelf life of the product (*167,168*). Similarly, the development of BC-based films and probiotic-derived bioactive metabolites (so-called postbiotics) has also gained attention for antimicrobial food packaging (*169,170*). For meat applications, the rapid release of postbiotics from BC-based films into food is ideal for food with a finite shelf life, as it can effectively control foodborne pathogens such as *Listeria monocytogenes* while also extending the shelf life without affecting the sensorial attributes of meat (*169,170*). In addition, several studies have performed *ex situ* and *in situ* modifications of BC to

improve its properties for use in food packaging. However, to assess its potential usefulness as active packaging, more research is needed to investigate the mechanical properties, permeability, interactions, and release rates in semisolid and solid food model media (*171*).

Other recent applications of BC include its use in dough leavening and baking trials to improve the rheological and sensory properties of gluten-free bakery products (*59*) and as a food-grade emulsion stabilizer (*172–174*), whose function can be extended to cosmetics and medical emulsions. In addition to the development of pH-sensitive indicators based on BC nanofibers incorporated with anthocyanins from various fruits, vegetables, and flowers to monitor the freshness and shelf life extension of fish (*175*), beverages (*176*), fruits (*177*), and shrimp (*178,179*).

CONCLUSIONS

AAB are well known for causing wine spoilage. However, their importance and functionality for food applications were demonstrated in this study. Through oxidative fermentation, AAB can produce a variety of metabolites. Its role in various biochemical processes during food fermentation, such as vinegar, kombucha, water kefir, cocoa, and lambic beer, the results in unique sensory and biochemical characteristics, as well as health benefits. Although the commercial production of vinegar-based drinks is well established, research on fruit drinks fermented by AAB is still relatively new and scarce. Beverage production of fruits through gluconic fermentation is very promising since several fruits can be used (including nonstandard fruits, for example) and can be more adaptable to AAB metabolism than to the growth of LAB. Furthermore, due to the formation of GA and the presence of phenolic compounds in the fruits, the functional drink could meet the demand of lactose intolerant, allergic to milk proteins, and those seeking a vegetarian, vegan and healthy diet. Due to its bioactive properties, levan could also be explored in beverage development. Levan could be produced *in situ* during the gluconic fermentation of fruit juices since several species of *Gluconobacter* can produce levan from sucrose and oxidize glucose to GA. BC has numerous applications in food, with several products already marketed worldwide. However, similar to levan, its main challenge lies in large-scale production and in reducing production costs to expand its applications in this area.

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CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

AUTHORS' CONTRIBUTION

Natália Norika Yassunaka Hata – processing/interpreting data, preparation of manuscript, and writing/revising the manuscript. Mônica Surek - writing/revising the manuscript. Daniele Sartori - processing/ interpreting data, preparation of manuscript, and writing/revising the manuscript. Rodrigo Vassoler Serrato - processing/interpreting data, preparation of manuscript, and writing/revising the manuscript. Wilma Aparecida Spinosa - processing/interpreting data, preparation of manuscript, and writing/revising the manuscript.

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Table 1. Acetic acid bacteria associated with fermented foods and beverages and with the synthesis of chemical compounds and polysaccharides

Food / Beverage / Chemical compounds / Polysaccharides	AAB species found associated with the fermentation	References
Vinegar		
Fruit vinegar (apple cider, orange, red and white wine, persimmon, white and red grape, apricot , and blueberry)	*A. pasteurianus, A. aceti, A. estunensis, A. pomorum, A. syzygii, K. europaeus, Novacetimonas hansenii (*formerly *K. hansenii), K. kakiaceti, K. oboediens, K. melaceti, K. melomenusus, N. pomaceti (*formerly *K. pomaceti), K. rhaeticus, K. saccharivorans, Gluconacetobacter (Ga.) entanii, N. maltaceti (formerly K. maltaceti), K. nataicola, K. intermedius, K. xylinus,* and *G. oxydans*	*1,7,22-27*
Cereal Vinegar (rice grain, wheat bran and rice hull, and glutinous rice)	*K. europaeus; K. kakiaceti,* and *K. medellinensis*	*27-29*
Cheese Whey vinegar	*A. aceti* and *A. pasteurianus*	*30,31*
Kombucha		
	A. papayae, A. indonesiensis, A. lovaniensis, A. okinawensis, A. peroxydans, A. syzgii, A. tropicalis, K. takamatsuzukensis, K. oboediens, K. eurapaeus, K. saccharivorans, K. intermedius, K. xylinus, K. rhaeticus, Novacetimonas hansenii (formerly *K. hansenii), Ga. liquefaciens, Ga. entanii, G. cerinus, G. oxydans,* and *Tanticharoemia sakaeratensis*	*32–37*
Water kefir		
	*A. indonesiensis, A. fabarum, A. orientalis, A. tropicalis, A. okinawensis, A. lovaniensis, A. lovaniensis, K. intermedius, K. saccharivorans, Novacetimonas hansenii (*formerly *K. hansenii), G. cerinus, G. japonicus,* and *G. liquefaciens*	*38-40*
Lambic beer		

	A. orientalis, G. cerevisiae, G. wancherniae, A. pasteurianus, A. aceti, A. lovaniensis,A. lambici, and *A. pomorum*	*41–43*
Cocoa		
	*A. pasteurianus, A. syzygii, A. tropicalis, A. ghanensis, A. indonesiensis, A. okinawensis, Novacetimonas hansenii (*formerly *K. hansenii), G. oxydans, G. frateurii, Gl. diazotrophicus,* and *Granulibacter bethesdensis*	*44-48*
Gluconic acid, Dihydroxyacetone, Vitamin C precursors, Miglitol		
	G. oxydans	*8,12,49,50*
New beverages from AAB		
	Acetobacter sp. and *G. japonicus*	*51-53*
Levan		
	*G. albidus, G.cerinus, G, oxydans, G. frateurii, Kozakia baliensis, Neoasaia chiangmaiensis, Tanticharoenia sakaeratensis, Novacetimonas hansenii (*formerly *K. hansenii), K. xylinus, A. pasteurianus,* and *Ga. diazotrophicus*	*54-58*
Bacterial cellulose		
	Novacetimonas hansenii (formerly *K. hansenii*), *K. nataicola*, *K. rhaeticus*, *K. swingsii*, *K. maltaceti*, and *K. xylinus*	*24,59,60*

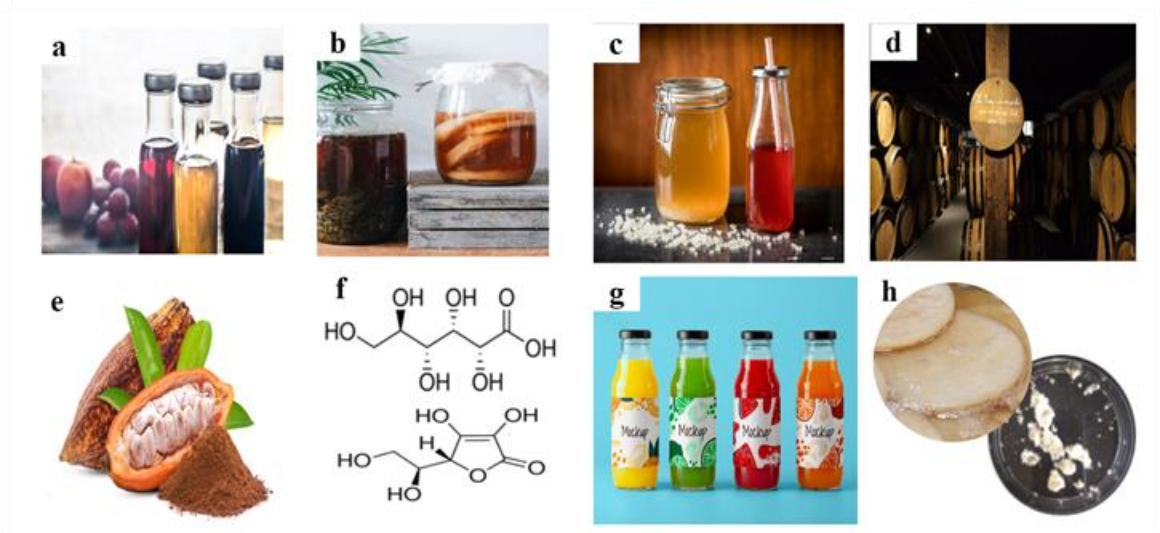
Fig. 1. Acetic acid bacteria are involved in various foods, beverages, chemicals, and exopolysaccharides. a) Vinegars from different raw materials; b) Kombucha; c) Water kefir; d) Lambic beer; e) Cocoa; f) Organic acids (gluconic and ascorbic); g) New fruit drinks; and Exopolysaccharides (bacterial cellulose and levan). Parts of the figure designed by iStock

Fig. 2. Chemical structure of levan

Fig. 3. Levan applications in food area. Parts of the figure designed by Freepik

Fig. 4. Chemical structure of bacterial cellulose

Fig. 5. Different applications of bacterial cellulose (BC) in the food industry. Parts of the figure designed by Freepik and iStock



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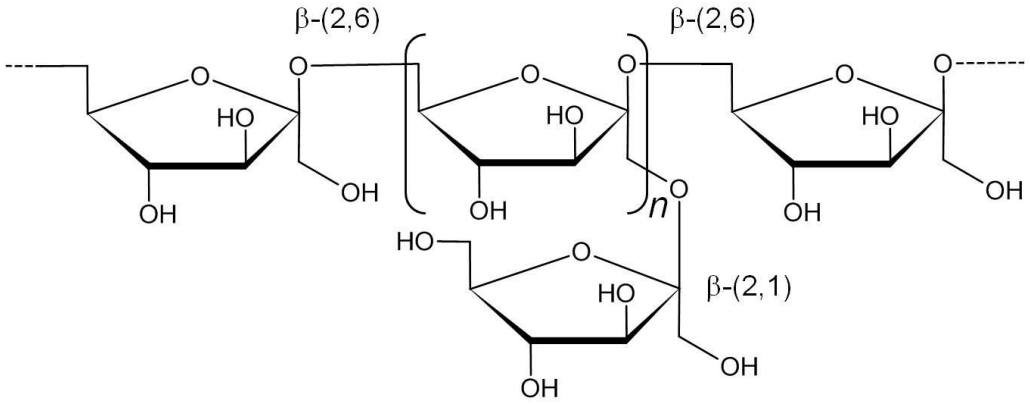

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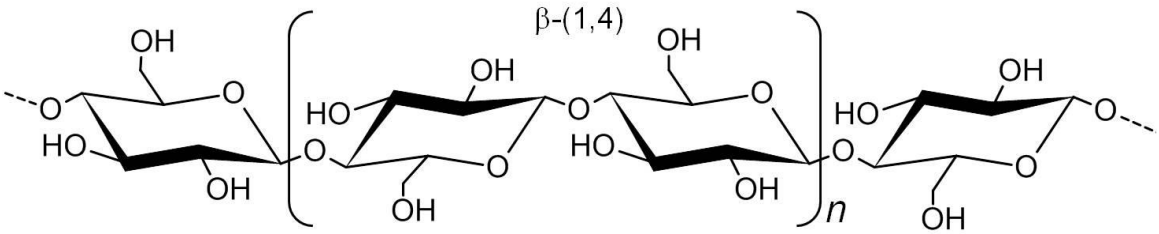

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