

Beets beyond sugar: Potential and limitations of sugar beet pulp as a feedstock for biorefineries

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ABSTRACT

Sugar beet (SB) is a major sugar crop in the European Union and the United States, primarily cultivated for the commercial production of table sugar. Post-extraction of sucrose, the fibrous fraction which remains is called sugar beet pulp (SBP). SBP is rich in structural carbohydrates such as cellulose, hemicellulose and pectin containing glucose, arabinose and galacturonic acid as their respective monomeric units. SBP is a renewable source of fermentable sugars that constitute about 85 % of total carbohydrates. Leveraging SBP as a substrate for a biorefinery supports circular bioeconomy principles by simultaneously reducing agricultural waste and enabling the sustainable production of value-added chemicals. This review highlights current advances in SBP valorization, beginning with an overview of SB processing and waste generation, followed by a critical assessment of pretreatment strategies that enhance carbohydrate accessibility. Particular attention is given to emerging routes for the bioconversion of arabinose and galacturonic acid, which together represent more than half of SBP's fermentable fraction yet remain significantly underutilized in industrial biotechnology. Microbial pathways, metabolic engineering interventions, and fermentation approaches enabling the production of value-added compounds such as arabinol, 2,3-butanediol, ascorbic acid, mucic acid and prebiotics are examined in detail. The review concludes by addressing current challenges and identifying research gaps to unlock the full potential of SBP within integrated biorefinery systems.

1. Introduction

The global dependence on fossil-based resources for the production

of fuels and chemicals has precipitated a series of interconnected challenges encompassing environmental, economic, and geopolitical dimensions. The extraction and usage of fossil fuels are the greatest

List of Abbreviations: 2G, Second generation; ACR, Agitated cell reactor; AD, Anaerobic digestion; AI, L-Arabinose isomerase; AL, Aldono-lactonase; ALDC, α -Acetolactate decarboxylase; AOS, Arabinooligosaccharides; DALS, α -Acetolactate synthase; ALX, L-Xylulose reductase; AR, L-Arabinose reductase; AsA, Ascorbic acid; BDH, Butanediol dehydrogenase; BDO, 2,3-Butanediol; COD, Chemical oxygen demand; DHA, 2-Keto-3-deoxy-D-lyxo heptulosaric acid; EME, Embden-Meyerhof pathway enzymes; FAO, Food and Agricultural Organization; G3P, Glyceraldehyde-3-Phosphate; GalA, Galacturonic acid; GAR1, D-Galacturonate reductase; GarD, Galactarate Dehydratase; GGP, GDP-L-galactose phosphorylase; GHG, Greenhouse gas; GLDH, L-Galactono-1,4-lactone dehydrogenase; HGA, Homogalacturonan; HK, Hexokinase; HMF, 5-Hydroxymethylfurfural; KDG, 2-Keto-3-deoxy-gluconate; KdGA, 2-Keto-3-deoxy-6-phosphogluconate aldose; KdGK, 2-Keto-3-deoxy-gluconate kinase; KDO, 2-Keto-3-deoxy-D-manno octulosonic acid; KDPG, 2-Keto-3-deoxy-6-phosphogluconate; LAD, L-Arabinol 4-dehydrogenase; LCB, Lignocellulosic biomass; LVS, Litre of volatile solids; LXR, L-Xylulose reductase; MAE, Microwave assisted hydrothermal extraction; OGAL, Oligogalacturonides; PDH, Pyruvate dehydrogenase; PHB, Poly(3-hydroxybutyrate); PK, Pyruvate kinase; POS, Pectic oligosaccharides; PPP, Pentose phosphate pathway; RG, Rhamnogalacturonan; RK, L-Ribulokinase; RPE, Ribulose-5-phosphate-4-epimerase; SB, Sugar beet; SBP, Sugar beet pulp; SCB, Sugarcane bagasse; TCA, Tricarboxylic acid; UdGH, D-Galacturonate dehydrogenase; UxaA, D-Altronate dehydratase; UxaB, D-Tagaturonate reductase; UxaC, Uronate isomerase; XDH, Xylitol dehydrogenase; XK, Xylulokinase.

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sources of greenhouse gas (GHG) emissions, linked with climate change, environmental degradation, exacerbating air and water pollution (Mujtaba et al., 2023; Schuetze and Hussein, 2023; Zoghalmi and Paës, 2019). It creates even greater challenges due to the fact that fossil fuel reserves are limited, creating a continual threat to resource availability and market stability, therefore increasing the need for alternatives. Not to mention, geopolitical hostilities over the fossil fuel deposits often lead to economic instability and energy uncertainty, adding more urgency to the transition towards renewable and locally sourced energy options (Wang et al., 2024).

Biorefineries hold the potential of resolving these challenges through the production of fuels, chemicals and materials from renewable biomass. Similar to traditional petroleum refineries, biorefineries bring together multiple operations in order to convert renewable feedstocks into high-value products for enhanced sustainability and circular use of resources (Calvo-Flores and Martin-Martinez, 2022). Based on the feedstock availability, the biorefinery concept is broadly classified into three generations that clearly outline progress in addressing concerns with respect to sustainability. First-generation biorefineries primarily utilize edible feedstocks such as corn, sugarcane, and vegetable oils. This feedstock is readily available and relatively easy to convert into biofuels and bioproducts through established biochemical processes like fermentation and transesterification (Barragán-Ocaña et al., 2023). However, significant drawback is being in direct competition with food production systems, thus making the food-versus-fuel debate all the more poignant (Buck et al., 2020). This concern is more important in those regions which are dealing with food insecurity or where using edible crops for industrial purposes can increase socio-economic disparities. Consequently, this limitation has spurred the development of second-generation biorefineries that focus on using non-edible, abundant and renewable feedstocks such as lignocellulosic biomass (LCB) and other agricultural byproducts, thereby aligning with ethical and environmental parameters. LCB is abundant and does not compete with food production, making it a promising substrate for sustainable bioeconomy development. However, the complex and recalcitrant structure of LCB poses significant challenges in conversion processes and necessitates fine-tuned pretreatment to extract fermentable sugars (Abolore et al., 2024). Despite these challenges, second-generation biorefineries hold substantial promises for sustainability due to their potential to integrate waste valorization within a circular bioeconomy framework. They offer environmental benefits by reducing waste disposal problems and GHG emissions, while promoting resource efficiency (Barragán-Ocaña et al., 2023; Buck et al., 2020). Furthermore, the pursuit of more sustainable and resource-efficient alternatives has led to the exploration of third-generation biorefineries, which capitalize on microbial cell factories to transform renewable energy and atmospheric CO₂ into fuels and chemicals (Liu et al., 2020). Within the third generation biorefinery, algal biomass (microalgae and macroalgae) serves as the primary feedstock and contains valuable fractions such as lipids suitable for biofuel production, proteins for animal feed applications, carbohydrates for fermentation processes, and specialized compounds with pharmaceutical or nutraceutical applications. Despite these promising attributes, third-generation biorefineries face significant economic barriers due to high operational costs associated with cultivation systems and harvesting technologies (Singh and Olsen, 2011). Moreover, current technological maturity remains limited compared to first- and second-generation approaches.

Considering the advantages and limitations of each generation of biorefinery systems in terms of sustainability, resource competition, technological maturity, and economic feasibility, LCB-based second-generation (2G) biorefineries stand out as promising platforms for sustainable bioeconomy development. Sugar beet (SB) is one of the major crops cultivated in several parts of world and grown commercially for sugar (sucrose) manufacturing, promoting an agriculture-based economy. The processing of SB after sugar extraction generates fibrous material called sugar beet pulp (SBP). SBP is an underutilized LCB and

being a rich source of fermentable and renewable carbon, it shows immense potential to serve as feedstock for 2G biorefineries. Due to increasing demand for sustainable resources for a vibrant bioeconomy, the valorisation of SBP has gained significant momentum in the last few decades. Unlike most conventional LCBs, SBP has a distinctive composition that is rich in arabinose and galacturonic acid, low in lignin, and contains a comparatively high protein fraction. These features make SBP particularly attractive for bioprocess development. Among the diverse range of feedstocks available, SBP emerges as a particularly valuable feedstock and serves as the central focus of this review. While glucose from SBP has been widely studied, the fermentative valorisation of other sugars like arabinose and galacturonic acid remains underdeveloped. This review therefore highlights strategies for the efficient bioconversion of these underutilized sugars, aiming to unlock their full potential for sustainable bio-based production. Towards the end, the review discusses associated challenges and identifies future research directions for enhanced circularity of SBP within the biorefinery systems.

2. Sugar beet-based sugar mills and associated waste streams

2.1. Sugar beet & production statistics

SB (*Beta vulgaris*) is a vital root crop grown for its high sugar content, mainly in Europe and North America. SB has the ability to thrive in cooler climatic conditions and cultivation of crops requires a specific environmental condition (temperate climates) and agronomic practices (loamy soil, well-draining, pH control) (Agronomic SB | Yara UK, 2019). It contains significantly high amounts of sucrose which makes it a valuable commodity for the sugar industries in various parts of the globe. SB is an alternative to sugarcane crop which thrives in tropical climates and contributes 20–25 % of global sugar production, whereas the remaining 75 – 80 % is obtained from sugar cane (Gruska et al., 2022; Varga et al., 2021). Both sugar cane and SB contain 15 – 20 % (w/w) of sucrose in their stem and root, respectively (Gruska et al., 2022; Sugar | alimentarium, 2016).

The total SB production across the globe was ~290 million tons in the year 2023, as reported by Food and Agricultural Organization (FAO) of the UN (FAOSTAT, 2024). A market analysis by Statista and IBIS World presented that the current SB production sector is valued at £ 223 million, and the revenue of the industrial sugar production is around £ 969.2 million with a projected CAGR of 3.65 % by 2027 (Industry Report, 2022; IBISWorld, 2023; Statista, 2023). Based on an analysis of the past three years data released by the FAO, it has been evident that Russia holds a substantial share of global SB production. France, USA, Germany, Turkey, Poland, Egypt, Ukraine, China, and the United Kingdom are the other major producers after Russia which produce a significant amount of SB ranging from 6 to 31 million tons per annum. The United Kingdom accommodates about 3 % of the world's SB production by utilizing around 0.5 % of its total agricultural land (Total agricultural land area UK 2022 | Statista, 2023; FAOSTAT, 2024). British Sugar is the main sugar-producing industry in the UK that processes around 8 million tons of SB to produce up to 1.2 million tons of sugar per annum (BritishSugar, 2023). The overall beet production statistics for the year 2023 are represented in Fig. 1.

2.2. Industrial production of sugar from sugar beet

After cleaning the harvested SB root, the procedure of sugar extraction starts with slicing the root into thin V-shaped strips (known as cossettes) that increase the surface area of the beet to process further. Cossettes are then placed in a multicell countercurrent diffuser filled with hot water, where ~98 % of beet sugar is extracted through osmosis in the form of “diffusion juice” or “raw juice”. The temperature inside the diffuser is maintained above 75 °C to reduce the chance of microbial contamination. Additionally, a brown sugary pulp is formed and transferred to another diffusion chamber to extract a possible amount of

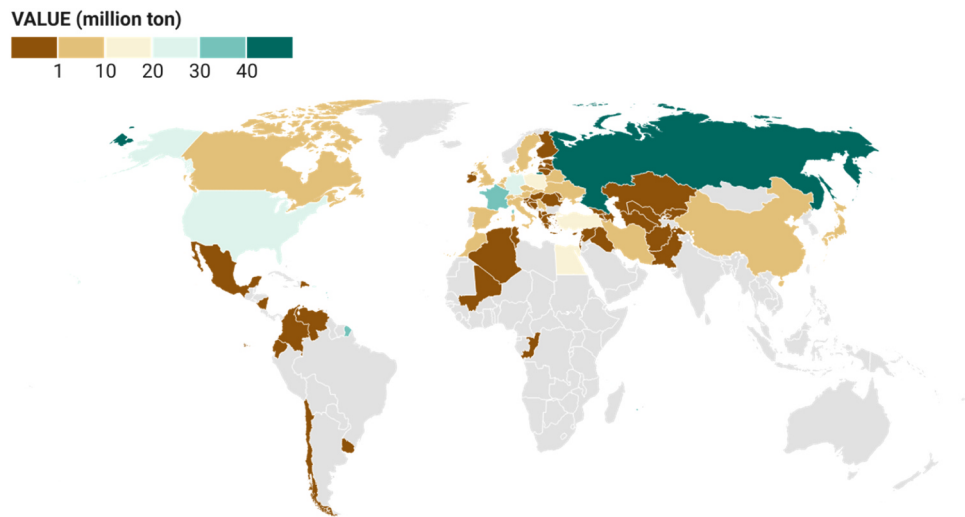


Fig. 1. Sugar beet production statistics (2023) (FAOSTAT, 2024).

residual sugar, which then leaves a brown non-sugary residue known as sugar SBP, retaining approximately 90 % moisture content (w/w, based on total weight) (Sugar - Beet | Britannica, 2024). Processing of one ton SB typically produces around 500 kg of wet SBP, which after pressing to reduce moisture content, yields approximately 50–70 kg of dry SBP (Tomaszewska et al., 2018; Marzo-Gago et al., 2023).

The raw juice is subjected to an initial purification by the addition of milk of lime and CO_2 . This leads to the formation of a calcium carbonate which precipitates along with the non-sugar residues, and the generated waste is commonly known as “lime solids” or “spent lime” (DeSutter and Godsey, 2010; The Sugar Series | Czarnikow, 2020). The composition of spent lime on wet basis (w/w) typically ranges from 50 to 57 % CaCO_3 , 30 % water, and 8 – 11 % SB impurities (organic matter), minerals, nitrogen, and phosphorous compounds depending on the individual characteristics of each processing batch (Ippolito et al., 2013). The elimination of these impurities results in the production of “thin juice” which has a higher purity level of sugar than raw juice. The thin juice undergoes a six-step evaporation process to form a thicker liquid which results in concentrating the sugar solution from ~16–65 % (The Sugar Series | Czarnikow, 2020). After this, a final four-phase crystallization process is employed for sugar crystallization. During the process of crystallization, a fudge-like highly viscous, deep brown byproduct is generated known as beet molasses (Djordjević et al., 2018). A pictorial representation of the sugar making process and the breakdown of different streams, showing the percentage contribution of each fraction is described in Fig. 2.

2.3. Waste streams generated after sugar extraction from SB and their current applications

This large-scale SB processing also generates substantial byproducts and waste streams, such as spent lime, SBP and molasses.

2.3.1. Spent lime

Spent lime, a byproduct generated during sugar extraction from SB finds its major application in the agricultural sector as a soil pH enhancer. When applied to soil, the calcium carbonate present in spent lime reacts with water to form a strong base $\text{Ca}(\text{OH})_2$, that neutralizes the soil acidity (DeSutter and Godsey, 2010; Adjusting low soil pH with spent lime, 2021). In a greenhouse study conducted by DeSutter and Godsey. (2010) incorporated three different types of lime source, where spent lime yielded the highest soil biomass and root mass compared to both reagent and commercial grade lime sources. In a few decades, numerous applications of spent lime have been explored. Dolignier and

Martin (1998) analyzed its usage in flue gas desulphurization, while Sahu highlighted its use within the sugar industries as an antimicrobial agent for sugar storage (Sahu, 2018). Furthermore, spent lime has been investigated as a sustainable alternative to mined calcium carbonate across various industries, potentially conserving natural resources. For instance, Vaccari et al. (1997) examined suitability of spent lime as a raw material in paper production, while Supaphol et al. (2004), Yang et al. (2006) and Zhang et al. (2004) explored its application in manufacturing composite materials and plastics. Li et al. (2013) and Sahu (2018) investigated spent lime as a filling material for construction materials and recent studies by Soydal et al. (2018) demonstrated enhancement of mechanical and thermal properties of epoxy-based composites using spent lime. Few other studies explored its use to remove hazardous synthetic colorants from the aqueous streams of textile, leather, food, and pharmaceutical industries (el Maguana et al., 2020; Marti and Zeidan, 2023).

2.3.2. Beet molasses

Sugar beet molasses is a byproduct of the sugar extraction process. It is known for its high content of fermentable sugars, proteins, and essential minerals. The composition includes dry matter, crude protein, ash, and total sugars (48 – 53 %), with specific mineral elements such as calcium, phosphorus, magnesium, potassium, sodium, chlorine, and sulfur. Fatty acid profiling of beet molasses shows the presence of palmitic, stearic, oleic, linoleic, and linolenic acids (Mordenti et al., 2021; Molasses, beet; Composition analysis, 2021). The energy values of beet molasses are significant, with a gross energy range of 2790–3690 kcal/kg, making it an excellent source of energy for livestock (Molasses, beet; Composition analysis, 2021). Beet molasses is widely used in animal nutrition as an energy source. It has positive effects on the production of milk fat, ruminal ammonia, and fiber digestibility in dairy cows. Due to its palatability, it is often added to animal diets to increase dry matter intake. In a study by Palmonari et al. (2020), the composition of sugar cane and beet molasses was characterized to highlight differences and provide an adequate definition of these foods. The study analyzed samples from around the world and found considerable variability in composition, even within the same group. This variability suggests that simply defining molasses by its origin is insufficient for accurately assessing its nutritional value.

2.3.3. Sugar beet pulp (SBP)

SBP is the fibrous residue obtained after the extraction of sucrose from SB. SBP is the major waste stream from sugar mills using SB as feedstock (Usmani et al., 2022). During the sugar making process,

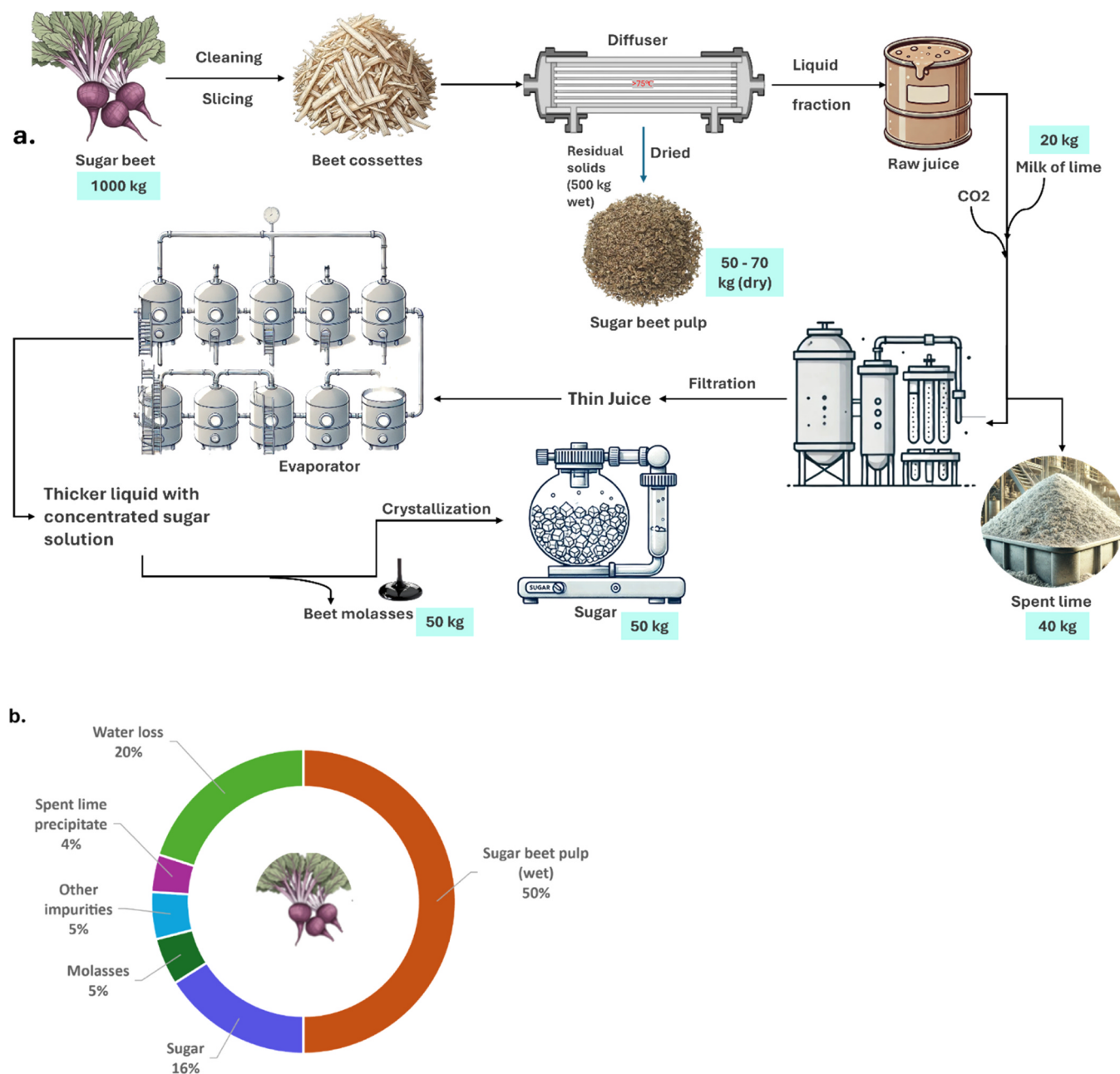


Fig. 2. **a)** Industrial sugar beet processing for sugar manufacturing, waste streams generated during the process and their quantitative distribution; **b)** breakdown of products and waste streams from processing sugar beet (Tomaszewska et al., 2018; Marzo-Gago et al., 2023).

approximately 50–70 kg of dry SBP is obtained after processing one ton SB (Tomaszewska et al., 2018). These SBPs are marketed in the form of pellets; however, this drying and pelleting process is energy-intensive and contributes significantly to the overall cost and environmental footprint of SBP handling. A typical composition of SBP is as follows: cellulose (22–30 %), hemicellulose (25–35 %), pectin (20–25 %), and lesser amounts of lignin (3–8 %), protein (10 %), and ash (3–5 %) (Ahmadi et al., 2015; Glaser et al., 2024) (Fig. 3). A distinguishing feature of SBP lies in its hemicellulosic and pectic composition. Unlike conventional LCBs, where hemicellulose is predominantly composed of xylan, SBP hemicellulose is rich in arabinan. Moreover, its high pectin content, largely composed of galacturonic acid as primary sugar, further sets it apart from typical LCBs. These polysaccharides on hydrolysis yield fermentable sugars. Cárdenas-Fernández et al. (2017) obtained the following composition of monosaccharides from acid hydrolysis of SBP: D-glucose (25.9 %), L-arabinose (23 %), D-galacturonic acid (14.4 %),

D-galactose (6.2 %), L-rhamnose (2.4 %), D-xylose (1.7 %), D-mannose (1.0 %) and others (25.4 %) (Fig. 4). Among the sugars derived from SBP, L-arabinose and D-galacturonic acid are of particular interest due to their distinct chemical properties and industrial relevance. L-arabinose is an aldopentose sugar while D-galacturonic acid is a six-carbon uronic acid derived from the oxidation of the C-6 hydroxyl group in D-galactose. Both sugars have diverse applications across pharmaceutical and food industries.

Currently, SBP is predominantly used as low-cost animal feed, despite its composition being rich in fermentable sugars such as arabinose and galacturonic acid. These sugars are not just common monosaccharides, they are high-value biochemicals and are precursors for specialty chemicals, pharmaceuticals, and cosmetic ingredients. In addition to its use as cattle feed, SBP is also processed through anaerobic digestion (AD), a microbial process that converts organic matter into biogas, primarily methane and carbon dioxide in an oxygen-free

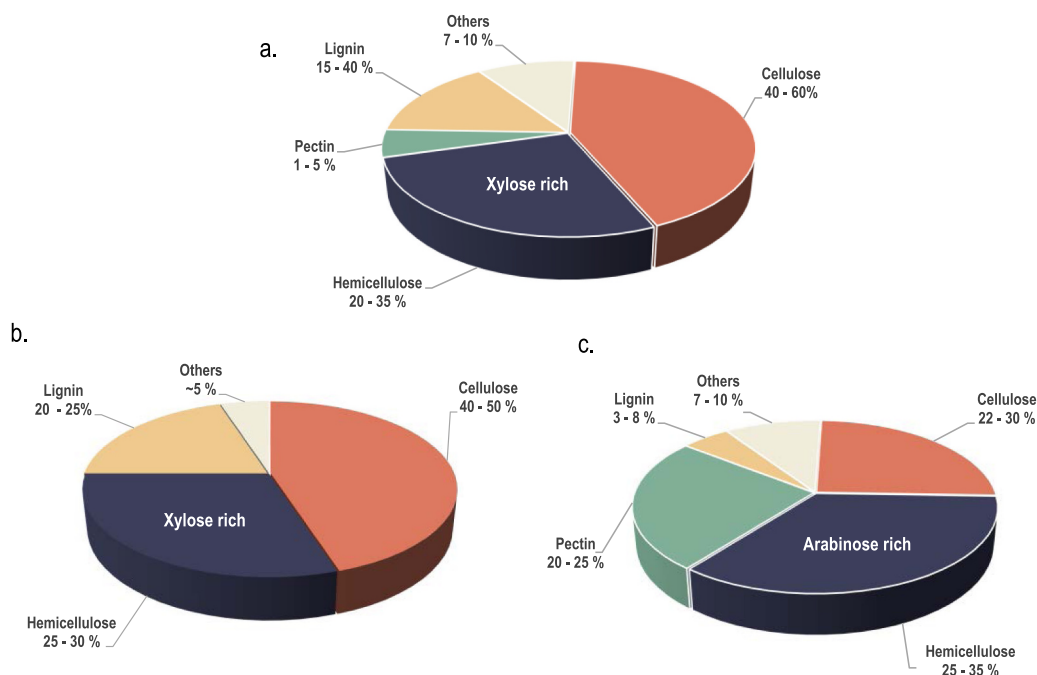


Fig. 3. Compositional comparison: a) Typical lignocellulosic biomass; b) Sugar cane bagasse; c) Sugar beet pulp (Rezende et al., 2011; Zoghiami and Paës, 2019; Glaser et al., 2024).

environment. In contrast, methane, the main product of AD, has a market value of just \$0.3–0.5 per kg (Methanol index - 2025), making it a far less economically attractive product from SBP. Yet, significant research continues to focus on biogas production from SBP. While AD is technically feasible and enables waste-to-energy conversion, it represents a low-value valorization pathway for a feedstock that contains inherently high-value components. A recent study by Pawlowska et al. (2023) investigated the requirement of a pretreatment step before carrying out AD. The results showed that alkaline pretreatment with NaOH (4 % w/w) at 22 °C was as effective as acid pretreatment with 10 % H₂SO₄ at 50 °C in terms of biomass solubilization, as indicated by similar dissolved chemical oxygen demand (COD) levels. Notably, the alkaline pretreatment at 22 °C emerged as the most economical option since it did not require heating and had lower NaOH consumption compared to H₂SO₄. Lemaigre et al. (2023) enhanced methane yields even under high ammonia conditions by acidifying with acetic acid, achieving 0.41 L_{CH₄}/L_{V_S}, while Elsayed et al. (2023) improved biogas output via co-digestion with sewage sludge at a 50:50 ratio. However, these strategies still culminate in methane, a bulk energy product with limited market value.

This discrepancy between the chemical potential of SBP and its current usage highlights a major underutilization of the resource. Instead of converting SBP into methane or feeding it to cattle, biorefinery-based approaches offer a far more promising and sustainable alternative by enabling the recovery of value-added products such as organic acids, alcohol, bioplastics, and platform chemicals. This review explores recent advances in unlocking the full potential of SBP through integrated biorefinery strategies aimed at high-value product generation.

3. Pretreatment of SBP: significance & strategies

SBP being rich in carbohydrates, shows great potential as a carbon source for the production of platform chemicals and various other products. However, its complex physicochemical composition, consisting of various interactions like hydrogen bonding, ester linkage, etc., requires precise pretreatment approach to harness its full potential (Faulon et al., 1994; Bellido et al., 2015; Dutra et al., 2018). Unlike a

typical LCB, SBP has a low lignin content. This makes the biomass more susceptible to enzymatic and microbial degradation. The outer layers of SBP are made out of pectin-rich matrix, predominantly composed of homogalacturonan (HGA) and rhamnogalacturonan regions, which include rhamnogalacturonan I (RG-I) and rhamnogalacturonan II (RG-II) (Niu et al., 2025). The HGA is a linear homopolymer composed of α -(1,4)-linked galacturonic acid that may be methyl-esterified or acetylated at varying degrees. The RG-I is a heteropolymer with a disaccharide backbone of alternating α -(1,2)-linked rhamnose and α -(1,4)-linked galacturonic acid residues. The RG-I structure also contains side chains which is rich in arabinose, galactose, and other neutral sugars. RG-II is a complex structure with rare sugars like 2-O-methyl xylose, 2-O-methyl fucose, aceric acid, 2-keto-3-deoxy-D-lyxo heptulosaric acid (DHA), and 2-keto-3-deoxy-D-manno octulosonic acid (KDO). This rhamnogalacturonan region of pectin is called as "hairy regions" (Ochoa-Villarreal et al., 2012; Mao et al., 2019; Jafarzadeh-Moghaddam et al., 2020). These pectic structures form a gel-like network, often cross-linked with calcium and other divalent cations to stabilize the cell wall architecture.

Unlike other LCB-based feedstocks where lignin creates an interwoven barrier around cellulose and hemicellulose, SBP's architecture relies on the interplay between pectin and hemicellulose with significantly lesser amount of lignin connections. Beneath the pectin layer, the hemicellulosic fraction acts as a reinforcing agent. This region is predominantly made up of arabinan, arabinogalactan, with a lesser amount of xyloglucan and are interconnected via β -(1,4) linkages (Whale et al., 2023; Chibrikov et al., 2024; Glaser et al., 2024). The hemicellulosic matrix is linked to cellulose microfibrils via hydrogen bonds (Whale et al., 2023). These cellulose microfibrils are composed of β -(1,4)-linked glucan chains stabilized by intra- and intermolecular hydrogen bonding, which results in a highly crystalline structure (Kannam et al., 2017). Following the disruption of this recalcitrant matrix, enzymatic hydrolysis requires carefully selected enzyme cocktails tailored to SBP's unique polysaccharide composition. Arabinofuranosidase and endo-arabinanase are key hemicellulases that degrade the arabinan-rich hemicellulose. For pectin breakdown, enzymes such as polygalacturonase, pectin lyase, and pectin methylesterase target the galacturonic acid backbone. Due to this complex composition, effectively

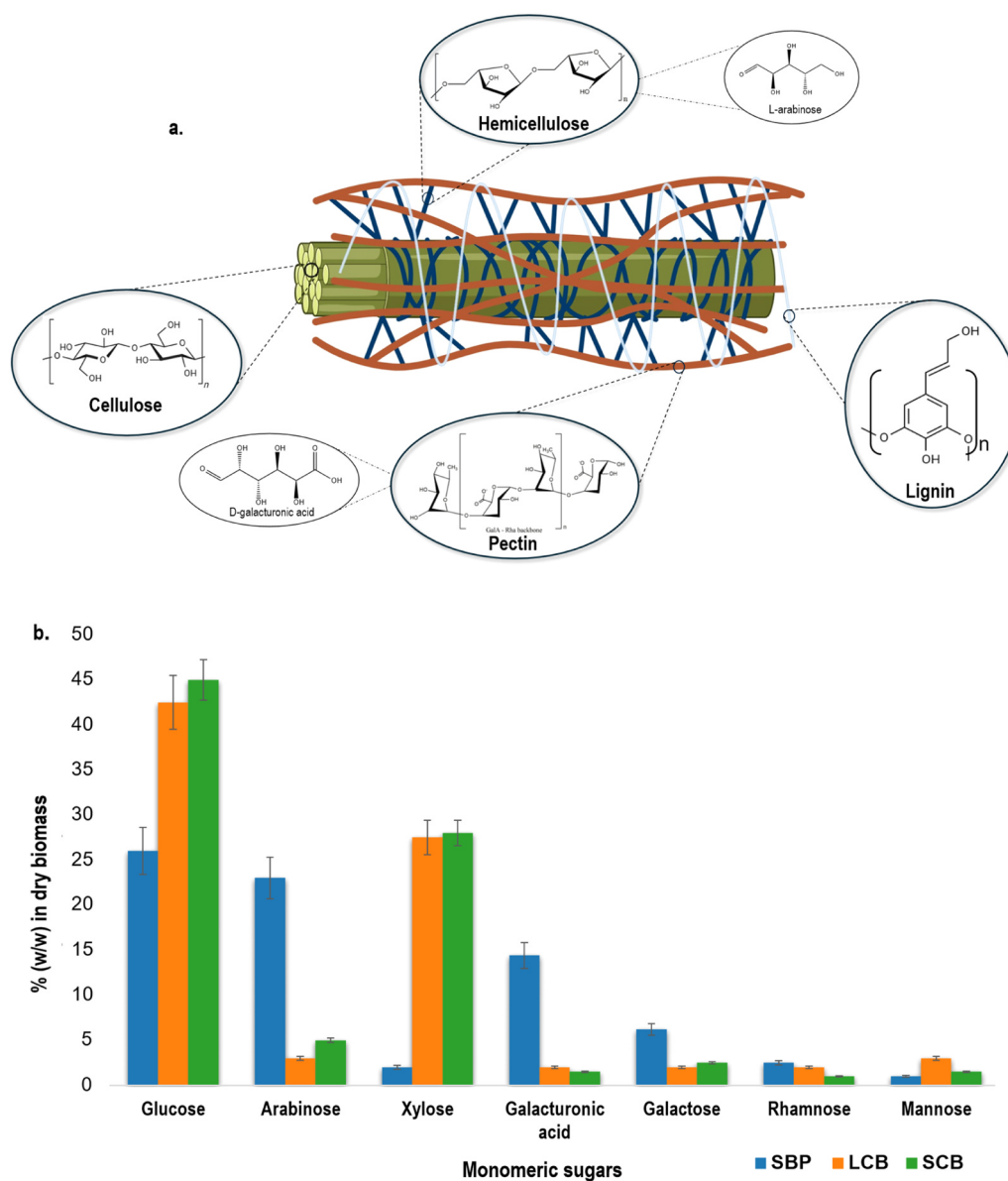


Fig. 4. a) Structural composition of SBP and chemical structures of dominant monomeric sugars from hemicellulose and pectin; b) Comparison of monomeric sugars in SBP, SCB and a typical LCB (Chiocchio, 2021; Rezende et al., 2011; Zoghalmi and Paës, 2019; Glaser et al., 2024).

breaking down SBP into fermentable sugars requires a well-designed pretreatment strategy. Various pretreatment methods have been explored to disrupt the pectin-hemicellulose-cellulose matrix, improve enzymatic accessibility, and enhance sugar release. These approaches range from chemical treatments, such as acid or alkaline hydrolysis, to enzymatic and physicochemical methods, each with its own advantages and limitations.

3.1. Aqueous ammonia

Aqueous ammonia pretreatment (AAP) is focused on exposing the cellulose fibers to enhance enzymatic digestion. The mechanism of action initiates with partial solubilization and deacetylation of the lignin matrix followed by partial hydrolysis of hemicellulosic linkages releasing fermentable sugars. This results in greater exposure of cellulose fibers for subsequent enzymatic hydrolysis. The effectiveness of this pretreatment depends on multiple factors viz., ammonia concentration, temperature, and residence time. Optimizing these parameters is crucial for maximizing the effect and minimizing the formation of any

inhibitory molecules like furfural and 5-hydroxymethylfurfural (HMF) (Jönsson and Martín, 2016). Ammoniation pretreatment works by blocking the methoxyl groups from absorbing cellulase by the lignin fraction (Li et al., 2017). In their study, SBP was subjected to 10 % AA pretreatment (solid: liquid = 1: 20 and a holding time of 6 h) at different temperatures namely 25, 40, 60 and 80 °C and later physicochemical characterization of the obtained pretreated SBP's was done to correlate it with enzyme digestibility. A pretreatment at 80 °C emerged to be the best pretreatment and was able to release 448.52 mg reducing sugars/g SBP (Li et al., 2017). Later, the same group did a comparative assessment of their optimized AAP with three other pretreatment strategies namely hydrochloric acid (HA), ammonium oxalate (AO) and pectinase to decipher which method resulted in maximum sugar release from SBP post enzymatic saccharification. The study revealed that AAP was the best as it disrupted ester linkages between carbohydrate and lignin, removing nearly 83.12 % and 66.32 % neutral detergent soluble (NDS) content and hemicellulosic fraction, respectively. Further, it facilitated cell wall dislocation and lignin redistribution. As a result, AAP pretreated SBP showed high specific surface area with high cellulose

content and crystallinity index resulting in maximum enzyme digestibility among all pretreatments. Compared to untreated SBP, AAP pretreated SBP released 173 % (487.8 mg/g versus 178.57 mg/g) more reducing sugars after 72 h of saccharification (Li et al., 2018). In their next study, they found that the AAP at relatively higher temperature (80 °C), not only improved the enzyme adsorption (37 % more than control) but also enhanced the catalytic efficiency (125 % more than control) of the enzyme, resulting in maximum sugar release during saccharification step. They attributed more exposure of hydroxyl groups and reduced decrystallization energy for promoting catalytic efficiency of the enzyme cocktail (Li et al., 2020). A recent investigation by Qian et al. (2023) provided a new route of valuable insight into the mechanism by which AAP enhanced the digestibility of SBP. Through comprehensive physicochemical characterization and glycome profiling, a method used to identify, quantify, and analyze the complete set of sugars present, the authors demonstrated that AAP at 80 °C for 3 h was sufficient to significantly enhance the enzymatic digestibility of SBP. This study identified arabinogalactans and rhamnogalacturonan epitopes as key contributors to recalcitrance, with their relative abundances negatively correlating with reducing sugar yields and positively correlating with biomass hardness and springiness (Qian et al., 2023).

3.2. Alkaline hydrolysis

Alkali pretreatment is an effective initial stage pretreatment for a typical LCB in the view of its delignification ability and modifying the structural components for further processing. This pretreatment employs alkaline reagents, such as sodium hydroxide, potassium hydroxide, calcium hydroxide, or alkaline hydrogen peroxide, to disrupt the lignin-carbohydrate complex and solubilize a significant portion of the lignin and hemicellulose fractions (Dutra et al., 2018). Shorter incubation time and lower temperature were the beneficial features of the alkali pretreatment (Pawłowska et al., 2023). Considering the fact that the SBP is a low lignin feedstock, alkali pretreatment has been found as a relatively lesser significant at a lower temperature. Hence researchers have found an alternative route in the usage of alkali conditions, such as alkali thermal pretreatment where the biomass is treated with NaOH at higher temperatures (at 100 °C), or by coupling alkali conditions with an addition of H₂O₂ at higher pH (11.5) and increased incubation time. These adaptations resulted in substantial benefits for further enzymatic hydrolysis by reducing the crystallinity of the cellulose matrix and effective delignification along with hemicellulose solubilization (Dutra et al., 2018; Marzo et al., 2021; Şenol et al., 2021). Moreover, in the context of biogas production through AD, Şenol et al. (2021) had concluded that the alkaline thermal treatment using KOH has increased the biogas yield by 171.72 %. The primary downside of using an elevated temperature is the increased likelihood of forming phenolic compounds, and sugar degradation products such as HMF, and furfural, which are known as fermentation inhibitors (Zheng et al., 2014).

3.3. Acid hydrolysis

Acid acting as a catalyst for breaking down the polysaccharide into simpler sugars is an attractive approach to yield the easily hydrolysable portion of biomass, subsequently breaking the recalcitrance structure for enzymatic hydrolysis (Kharina et al., 2016). Researchers have been exploring the route of acid hydrolysis using multiple acids such as sulfuric acid, hydrochloric acid, sulfurous acid, phosphoric acid, citric acid, and found that each has its advantage for further processing (Chamy et al., 1994; Ivetic et al., 2016; Gönen et al., 2023; Türk et al., 2023). For instance, treating SBP with phosphoric acid increased the cation removal capacity and provided a significant boost to the color lightning property (Türk et al., 2023). Kharina et al. (2016) found that the usage of a relatively low amount of sulfurous acid (~1 %) in combination with a low solid-to-liquid ratio (1:3, 1:6) and lesser incubation time (10 – 20 min) resulted in the release of about 33 % of total carbohydrate and

aided significantly in the further enzymatic hydrolysis yielding a total of 90 % glucose combined (Kharina et al., 2016). El-Gendy et al. (2015) optimized the usage of hydrochloric acid for SBP treatment using RSM and found that at a solid loading of 15 % (w/w) and acid loading of 0.1 N HCl with an incubation time of 6 min under pressurized conditions at 120 °C resulted in ~30 % saccharification yield of SBP. It has also been noted that using a high concentration of HCl (>0.5 N) under severe conditions caused an increased weight loss of SBP with lower sugar yields, indicating potential sugar degradation (El-Gendy et al., 2015). Sulfuric acid is most commonly used for acid pretreatment of any type of LCB due to its ability to extract higher sugar yield with lower costs, which is fundamental for economic success (Mussatto, 2016). The acid hydrolysate of SBP majorly contains arabinose and xylose indicating the efficient hydrolysis of hemicellulose and a fraction of pectin regions (Chamy et al., 1994; Berłowska et al., 2018; Pawłowska et al., 2023). Alexandri et al. (2019) attempted complete fractionation of SBP in which first phase involved the extraction of phenolics and pectin. In the second phase two different acids were used for pretreatment (121 °C for 15 min) where 0.5 % (v/v) sulfuric acid emerged to be the best. Later solid loadings and pretreatment duration were optimized by the group. A solid loading of 10 % and pretreatment time of 30 min facilitated 79.1 % hydrolysis of hemicellulosic fraction (37.03 g/L reducing sugars), with arabinose being most predominant sugar followed by glucose, fructose (monosaccharides from sucrose hydrolysis) and galactose. Their two-way ANOVA study revealed that solid loading had a significant effect on hemicellulose hydrolysis whereas duration of pretreatment was insignificant.

Recently Glaser et al. (2024) also conducted studies with hydrochloric acid and sulfuric acid to decipher the suitability of acid and pretreatment conditions. Their study showed that 0.64 M sulfuric acid treatment at 80 °C for 7 h resulted in selective solubilization of 80 % arabinose with no substantial loss of glucose or any other sugars. Even though the usage of acids aids in the efficient release of fermentable sugars and enhances enzymatic hydrolysis, this process also generates a significant amount of fermentation inhibitors such as furfural and HMF coming from degradation of C5 and C6 sugars, respectively (Chamy et al., 1994; Zheng et al., 2012; Pawłowska et al., 2023).

3.4. Other pretreatment strategies

In addition to already mentioned pretreatment strategies. Several other methods have been explored to disrupt the linkages in SBP and extract sugars from it for valorization purpose. Among these, hydrothermal, steam explosion, and continuous flow pretreatments have gained attention for their ability to enhance sugar release without relying on additional chemical reagents. These methods primarily focus on altering the structural integrity of SBP to improve enzymatic accessibility and downstream processing efficiency. Hydrothermal pretreatment has emerged as one of the environmentally friendly methods for SBP, using only water at elevated temperatures without chemical additives. Studies examining the effects of liquid hot water (LHW) treatment on SBP at temperatures ranging from 120 to 200 °C found that the highest concentration of free glucose (3.29 mg/ml) was observed at 160 °C, which was 4-fold higher than processing at 120 °C (Ziemiński et al., 2014). A study by Kühnel et al. (2011) achieved 60 % w/w solubilization of total carbohydrates (predominantly pectin) in SBP with an optimal pretreatment condition of 140 °C for 15 min in water (Kühnel et al., 2011). Chen et al. (2015) optimized this technique for efficient pectin extraction and found that a liquid-to-solid ratio of 44.03 %, a temperature of 120.7 °C, an extraction time of 30 min, and a pressure of 10.7 MPa resulted in a pectin yield of 24.6 % (Chen et al., 2015).

Steam explosion uses high-pressure saturated steam followed by sudden decompression, causing the material to undergo explosive decompression. This process has been optimized for SBP, with studies identifying optimal conditions of 5.3 bar pressure and 24.4 min of treatment time. These conditions allow for selective extraction of SB

pectin and hemicellulosic fraction yielding around 83.2 % arabinose release while leaving most of the cellulose fraction intact (Cárdenas-Fernández et al., 2017). Morphological analysis has demonstrated that steam-explosion pretreatment largely extracts the binder materials of hemicellulose and pectin, exposing the micro fibrillated cellulosic fibers (Yang et al., 2018). Despite its effectiveness, steam explosion can produce inhibitory byproducts that may be toxic for subsequent valorization processes, including weak acids, furan derivatives, and phenolic compounds (Zhao et al., 2023). Additionally, the process requires specialized equipment capable of handling high pressures and temperatures, which may limit its application in smaller-scale operations.

Innovative continuous pretreatment systems have been developed to overcome limitations of batch processes for SBP processing. The agitated cell reactor (ACR), a 100 ml continuous flow reactor, has shown excellent plug flow properties and well-mixed conditions, optimizing reaction kinetics, equivalent to 13 stirred reactors in series, and can handle SBP slurries over a range of solids loadings (1–5 % w/v) (Chiocchio, 2021). Studies on particle flow through the ACR demonstrated that steady state could be achieved, though larger particles had longer residence times than smaller particles. When comparing continuous flow dilute acid pretreatment in the ACR to steam explosion pretreatment, similar throughputs were obtained (3.1 and 3.5 g_{ara}/hr, respectively), but productivity was an order of magnitude higher in the ACR (25.6 vs 3.5 g_{ara}/L/hr). Another innovative approach is the FASTSUGARS process, which combines supercritical water as hydrolysis medium with short reaction times in ultrafast reactors. Operating at 390 °C, 25 MPa, and reaction times between 0.11 and 1.15 s, this process can convert SBP into sugars with the highest yields of C6 and C5 sugars (61 % and 71 % w/w, respectively) obtained at 0.11 s (Martínez et al., 2018). Despite these advancements, continuous flow pretreatment systems still encounter challenges such as clogging risks with high-solids feedstocks, difficulty in maintaining consistent residence time distribution for heterogeneous materials, and the requirement for specialized equipment, which can require substantial capital investment for industrial-scale implementation. A summary of pretreatment methods is presented in Table 1.

Recent process innovations have also prioritized SBP as a feedstock for prebiotic production, particularly targeting the release of pectic oligosaccharides (POS), arabinan, and galactan oligosaccharides—compounds with validated prebiotic effects. Hydrothermal and microwave-assisted hydrothermal extractions, as detailed above, are now recognized not only for efficient sugar and pectin release but also for generating high yields of low-degree polymerization oligosaccharides, which selectively stimulate beneficial gut microbes (e.g., *Bifidobacterium*, *Lactobacillus*) (Dou et al., 2025). Del Amo-Mateos et al. (2022) optimized microwave assisted hydrothermal extraction (MAE) that favored maximum release of POS and later the pretreated SBP was enzymatically digested to produce hydrolysate which was then valorized to bio-butanol. A temperature of 165 °C with a holding time of

12 min was found optimum and achieved extraction yield of 33.4 % (g_{POS}/g_{SBP}) claiming formation of no degradation products. A two-step, non-isothermal hydrothermal process has been demonstrated by Martínez-Gómez et al. (2024) for separately generating streams enriched in oligogalacturonides (OGaLA) and arabinooligosaccharides (AOS), each with high purity after membrane filtration or ion-exchange refinement. Operating first at 130 °C yields up to 30 % (w/w) OGaLA, while a subsequent step at 175 °C delivers up to 37.5 % (w/w) AOS; downstream processing further concentrated these fractions with refined products comprising 42.5 % (w/w) OGaLA or 55 % (w/w) AOS, respectively. Prandi et al. (2018) used a two-step process; extraction and hydrolysis-based treatment of SBP to achieve efficient production of POS. Nitric acid at pH 1.4 and 80 °C was used for pectin extraction, followed by enzymatic hydrolysis using Viscozyme L (endo- and exo-galacturonase enzyme blend) in an enzyme membrane reactor. Low to medium molecular weight cut-off membranes (10–30 kDa) was used during hydrolysis, that enabled the production of POS fractions dominated by short-chain arabinan oligomers, with more than 70 % arabinan and galacturonic acid content. Overall, the continual advancements in pretreatment technologies have not only improved the efficiency of sugar and pectin extraction from SBP but also created new opportunities for generating high-value products, such as prebiotic oligosaccharides, tailored to both health and industrial markets. These innovations underscore the versatility of SBP as a renewable feedstock and highlight how optimized pretreatment can serve as a critical gateway, directing the subsequent conversion of the resulting structural sugars and oligosaccharides into a diverse array of biochemicals, prebiotics, and fuels.

The upcoming section exclusively discusses the efforts made by various researchers to valorize distinct types of sugars extracted from SBP (e.g. arabinose, galacturonic acid, glucose and xylose) and produce an array of industrially important products from them. Since the percentage of arabinose (monomeric form) as hemicellulose component is relatively higher compared to other LCB's and galacturonic acid (monomeric form of pectin) is unique to SBP, microbial pathways to metabolize them and valorize them to various chemicals are discussed in detail.

4. Arabinose

4.1. Metabolism

Arabinose (C₅H₁₀O₅) is an aldopentose sugar and a major monosaccharide component of the SBP. It exists predominantly in two stereoisomeric forms: L-arabinose and D-arabinose, with the L-arabinose form being more prevalent in nature (Kumar et al., 2023). It has a sweetness level of approximately 50 % that of sucrose, making it a potential low-calorie sweetener. Moreover, L-arabinose is recognized for its ability to inhibit intestinal sucrase activity through non-competitive binding, thereby reducing the absorption of sucrose and the magnitude of hyperglycemia (Pol et al., 2022). Building on these properties,

Table 1
Summary of various pretreatment methods.

Method of pretreatment	Process conditions	Result	Mode of Action	Reference
Ammonia fibre expansion	10 % wt – aqueous ammonia at 80 °C	37 % increase in cellulase adsorption to pretreated SBP compared to untreated	Exposing the cellulose fibers and redistributing linin to enhance enzymatic digestion	Li et al. (2017)
Dilute acid treatment	2 % v/v H ₂ SO ₄ at 121 °C for 15 min	0.18 g/g _{SBP} of arabinose release	Pectin and hemicellulose solubilization and cellulose exposure for enzymatic digestion	Narisetty et al. (2022)
Alkaline hydrogen peroxide treatment	1 % w/v H ₂ O ₂ at pH 11.5 & 25 °C for 18–24 h	Complete delignification	Removal of lignin, partial solubilization of hemicellulose and reducing the crystallinity of the cellulose matrix	Ho et al. (2019)
Hydrothermal pretreatment	120 – 200 °C for 20 min	Complete galacturonic acid and 80 % arabinose solubilization	Complete pectin and partial hemicellulose solubilisation	Ziemiński et al. (2014)
Steam explosion	150 – 180 °C at 5 bar for 24 min	90 % (w/w) L-arabinose, 44 % (w/w) D-galacturonic acid, 5 % (w/w) D-glucose release	Pectin and hemicellulose solubilization	Hamley-Bennett et al. (2016)

arabinose also holds significant potential in the realm of fermentation. Understanding the metabolic pathways of arabinose is crucial for optimizing its use in biotechnological applications. The metabolism and uptake route of arabinose is different in different classes of organisms. In bacteria like *E. coli*, arabinose uptake is mediated by three distinct transport systems that differ in affinity and energy dependence. The *AraFGH* system, a high-affinity ATP-binding cassette (ABC) transporter, serves as the primary mechanism for arabinose import, especially under

low substrate concentrations. In this system, *AraF* encodes the periplasmic arabinose-binding protein, *AraH* forms the membrane component, and *AraG* functions as the ATP-binding module required for active transport. In addition to this, *E. coli* possesses a lower-affinity transporter, *AraE*, which is a proton symporter and facilitates arabinose uptake under higher extracellular concentrations (Brown and Hogg, 1972). More recently, *AraJ* has been identified as a potential arabinose transporter. Although its precise physiological role remains to be fully

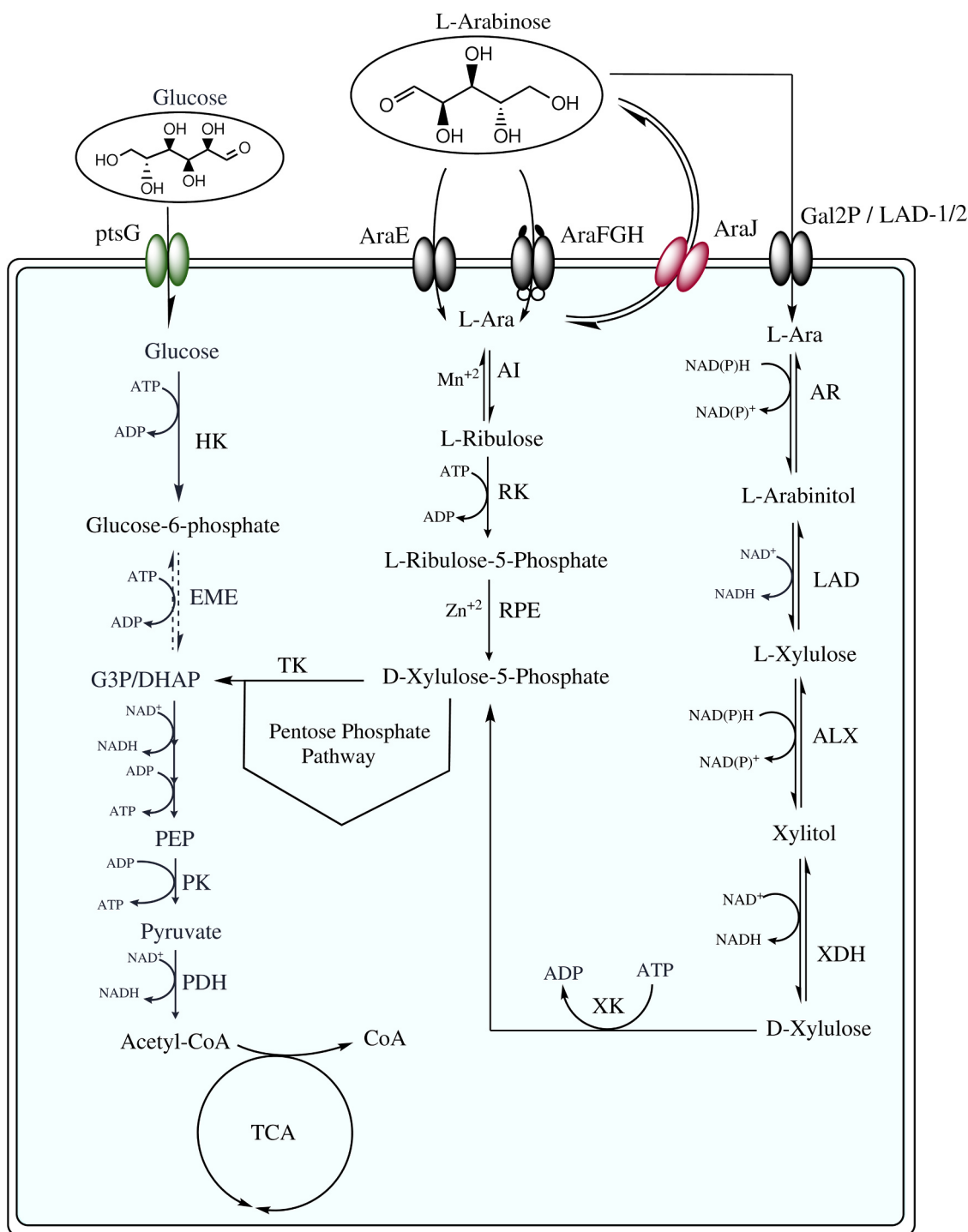


Fig. 5. Biochemical pathways for arabinose metabolism in prokaryotes (middle) and eukaryotes (right) along with glycolysis(left). **HK** Hexokinase; **EME** Embden-Meyerhof pathway enzymes; **PK** Pyruvate kinase; **TCA** Tricarboxylic acid; **AI** L-Arabinose isomerase; **RK** L-Ribulokinase; **RPE** Ribulose-5-phosphate-4-epimerase; **PDH** Pyruvate dehydrogenase; **AR** L-Arabinose reductase; **LAD** L-Arabinitol 4-dehydrogenase; **ALX** L-Xylulose reductase; **XDH** Xylitol dehydrogenase; **XK** Xylulokinase.

elucidated, AraJ is predicted to be an inner membrane protein belonging to the drug: H⁺ antiporter 1 (DHA1) family within the major facilitator superfamily (MFS), suggesting a possible role in maintaining intracellular arabinose homeostasis (Desai and Rao, 2010; Schleif, 2010; Ranade and He, 2021). In yeasts, arabinose transport is facilitated by a variety of transporters, each with distinct substrate specificities, affinities, and mechanisms. In *Saccharomyces cerevisiae*, the native galactose permease (*Gal2p*) has been shown to transport L-arabinose, albeit with low efficiency (Wang et al., 2017). In non-conventional yeasts like *Kluyveromyces marxianus* and *Pichia guilliermondii*, specific arabinose

transporters such as *KmLAT1* and *PgLAT2* have been identified (Zhang, 2013). Whereas filamentous fungal transporters such as *LAT-1* from *Neurospora crassa* and *MtLAT-1* from *Myceliophthora thermophila* have been characterized as low-affinity, high-capacity proton-coupled symporters for arabinose uptake (Li et al., 2015).

Following its transport into the cell, arabinose enters organism-specific metabolic pathways that convert it into intermediates suitable for central carbon metabolism (Fig. 5). In prokaryotes, the arabinose utilization pathway initiates with the conversion of L-arabinose to L-ribulose by the enzyme L-arabinose isomerase (*AraA/AI*). The L-ribulose

Table 2

Various fermentative bioproducts using different carbon sources present in SBP.

Fermentative product	Pretreatment approach of SBP	Dominant sugars in hydrolysate	Organism	Genotype	Titer (g/L)	Yield (g/g)	Productivity (g/L/h)	Ref
Ethanol	Thermal (20 min 121 °C) + Enzymatic (cellulase + pectinase)	Glucose, Galactose and Galacturonic acid	<i>S. cerevisiae</i>	Wild type	2.35	0.25	0.29	Rezicó et al. (2013)
	Pressure-thermal (prior soaked in 2 % w/w H ₂ SO ₄) + Enzymatic (Viscozyme + Ultraflo Max)	Glucose, xylose, arabinose, galacturonic acid	<i>S. cerevisiae</i> (Ethanol Red)	Engineered	26.9	0.43	0.373	Berłowska et al. (2016)
	Dilute acid treatment + Fungal enzyme solid state enzymatic hydrolysis	Glucose	<i>S. cerevisiae</i> Y39	Wild type	48	0.32	0.8	El-Gendy et al. (2015)
Acetone-Butanol-Ethanol (ABE)	Liquid hot water at pH 4 + Enzymatic (cellulase + β-glucosidase + pectinase)	Glucose, fructose, and arabinose	<i>Clostridium acetobutylicum</i>	Wild type	11.7 (acetone + butanol)	0.4	0.097	Bellido et al. (2015)
	Microwave assisted hydrothermal extraction followed by enzymatic hydrolysis with Cellic CTec2	Glucose followed by Arabinose and Galactose	<i>Clostridium beijerinckii</i> DSM 6422,	Wild type	8.3 (butanol) 15.2 (ABE)	-	0.17 (butanol) 0.32 (ABE)	del Amo-Mateos et al. (2022)
	Simultaneous saccharification and fermentation (pre hydrolysis for 10 h using Viscozyme and Ultraflo Max)	Arabinose, Galactose, Raffinose	<i>Lactococcus lactis</i> PCM 2379	Wild type	30	-	0.625	Berłowska et al. (2018)
Lactic acid		Arabinose, Galactose, Raffinose	<i>Lactobacillus plantarum</i> HII + <i>L. brevis</i> PCM 488 (co-culture)	Wild type	55.79	-	0.58	Berłowska et al. (2016)
	Dilute sulfuric acid hydrolysis and enzymatic saccharification	Glucose, xylose and arabinose	<i>Bacillus coagulans</i> A166	Wild type	29.14 (Continuous culture)	0.73	1.21	de Oliveira et al. (2020)
	Dilute sulfuric acid pretreatment (1 % w/w) followed by enzymatic saccharification	Glucose followed by Arabinose and Galactose	<i>Lactiplantibacillus plantarum</i>	Wild type	50	-	0.23	Marzo et al. (2021)
Arabitol	Dilute sulfuric acid treatment at 200 °C for 1 min	Arabinose followed by xylose and glucose	<i>Spathaspora passalidarum</i> CBS 10155	Wild type	8.48	0.603	0.176	Novak et al. (2024)
	Hydrothermal treatment at 170 °C followed by dilute acid hydrolysis using 0.5 % v/v H ₂ SO ₄ at 121 °C for 165 min	Arabinose	<i>S. cerevisiae</i>	Engineered native GRE3↑ + GAL2↑	14.5	1.00	0.35	Baptista et al. (2024)
Succinic acid	Acidified aqueous ethanol extraction followed by dilute sulfuric acid hydrolysis and enzymatic saccharification	Glucose and Arabinose followed by fructose and galactose	<i>Actinobacillus succinogenes</i> DSM 22257	Wild type	30 (Fed-batch at pilot scale)	0.90	0.75	Alexandri et al. (2019)
Polyhydroxybutyrate (PHB)	Aqueous extraction followed by pectin extraction using dilute sulfuric acid. Later hydrothermal pretreatment followed by enzymatic hydrolysis	Glucose followed by xylose, arabinose, mannose and galactose	<i>Paraburkholderia sacchari</i>	Wild type	62.2	0.27	1.71	Sarafidou et al. (2024)
D-galactone	Autoclave in potassium citrate buffer for 20 min + Enzymatic hydrolysis of pectin using pectinase from <i>A. niger</i>	Galacturonic acid	<i>S. cerevisiae</i>	Engineered GalUR ↑	9.9	0.66	0.19	Wagner et al. (2021)

↑ - Overexpression

formed is phosphorylated by L-ribulokinase (*AraB/RK*) and results in the formation of ribulose-5-phosphate. The L-ribulose-5-phosphate is converted to D-xylulose-5-phosphate by ribulose-5-phosphate-4-epimerase (*AraD/RPE*) enzyme which successively enters carbon metabolism via pentose phosphate pathway (PPP). This route of arabinose metabolism is redox-neutral, indicating that it remains unaffected by any cofactor imbalances. The second route of arabinose assimilation is seen in organisms like yeast and fungus which is an oxido-reductive pathway. This route is dependent on both the cofactors NAD(P)^+ and NAD(P)H and unlike the bacterial route of arabinose metabolism, the fungal pathway is significantly affected by the availability of redox cofactors. The process involves four alternating reduction-oxidation reactions catalyzed by L-arabinose reductase (*AR*), L-arabinitol 4-dehydrogenase (*LAD*), L-xylulose reductase (*ALX* or *LXR*), and xylitol dehydrogenase (*XDH*), followed by a phosphorylation step catalyzed by (*XK*). The pathway converts L-arabinose to L-arabinitol (using NADPH), then to L-xylulose (using NAD^+), followed by conversion to xylitol (using NADPH), and finally to D-xylulose (using NAD^+), before phosphorylation to D-xylulose 5-phosphate. This pathway has been well-characterized in fungi such as *Aspergillus niger* and *Trichoderma reesei*, as well as in some yeasts like *Pichia stipitis*. Interestingly, it converges with the D-xylose utilization pathway at the xylitol step, which has implications for the co-utilization of these pentose sugars in metabolic engineering efforts (Richard et al., 2003; Seiboth et al., 2011; Metz et al., 2013; Kumar et al., 2023).

4.2. Fermentative utilization of SBP-arabinose for sustainable biochemical production

4.2.1. Arabitol

Arabitrol, sugar alcohol (pentitol family), is increasingly recognized for its applications in the food industry as a low-calorie and low-insulinemic sweetener with about 70 % of the sweetness of sucrose and an energy density of 0.2 kcal/g, and in pharmaceuticals as an anti-cariogenic agent and adipose tissue reducer (Kordowska-Wiater et al., 2017a; Sundaramoorthy and Gummadi, 2019). Arabitol as a precursor, can also be used as a substrate for the production of various value-added chemicals viz., xylitol, ethylene glycol, arabionic acid, xylonic acid, etc (Kordowska-Wiater, 2015a). The present industrial production of D-arabitrol follows a two-step hydrogenation process using arabinoic acid and its lactone (a cyclic ester) as intermediates. The process begins with conversion of arabionic acid, derived from arabinose, into arabinono-1,2-lactone through cyclization. In second step, the lactone undergoes hydrogenation in the presence of molecular hydrogen and Raney nickel catalyst at high temperatures and pressures (typically 100–150 °C & 30–60 bar) to form D-arabitrol (Ravikumar et al., 2022; Kumar et al., 2023). However, this process is limited by its high energy demands and the cost of the catalyst. The biological production of arabitol has been explored using different native strains such as *Scheffersomyces shehatae*, *Candida quercitrusa*, *Zygosaccharomyces siamensis* kiy1, *Pichia mancharica*, *P. guilliermondii*, *C. parapsilosis*, *Debaryomyces* sp. etc using various sugars (Yoshikawa et al., 2014; Kordowska-Wiater et al., 2017b, 2017c; Sundaramoorthy and Gummadi, 2019; Iwata et al., 2023). There are only two isolated studies wherein researchers have attempted to valorize the arabinose fraction of SB for bioproduction of arabitol (Table 2). For instance, Novak et al. (2024) used SBP as feed-stock for arabitol production. In their study, the SBP were subjected to dilute sulfuric acid pretreatment and the arabinose-rich hydrolysate obtained was then valorized to arabitol using *Spathaspora passalidarum* CBS 10155. The yeast assimilated acetic acid as well, besides arabinose and produced 8.48 g/L of arabitol. A recent study by Baptista and colleagues highlighted the potential of a genome-edited *S. cerevisiae* strain, engineered to overexpress only homologous genes, for producing arabitol using arabinose derived from SBP (Baptista et al., 2024). They used CRISPR/Cas9 chromosomal integration to overexpress native *GRE3* and *GAL2* encoding NADPH-dependent aldose reductase and galactose

permease, respectively. This genetic modification significantly enhanced arabinose transport and metabolic conversion, resulting in a 1.95-fold increase in arabitol productivity. The engineered strain achieved an arabitol titer of 15 g/L with a yield of 1.0 g/g, reaching the theoretical maximum when utilizing non-detoxified SBP hydrolysate as the primary arabinose-rich carbon source. In a rare study, Knesbeck et al. (2024) tested the performance of a genetically modified *A. niger* NRRL3 for biotransformation of arabinose sugar to xylitol. They generated sugar-hydrolysate by growing *A. niger* strain on SBP under solid state fermentation conditions. After hydrolysis, the hydrolysate was subjected to charcoal treatment and centrifuged to obtain a clear hydrolysate.

The advancements in microbial and enzymatic strategies for arabitol biosynthesis highlight a promising shift toward sustainable and cost-effective production. By leveraging metabolic engineering to optimize strains and innovative bioreactor designs for substrate valorization, researchers have achieved remarkable titers and conversion efficiencies. While challenges such as redox cofactor imbalances and process scalability persist, the integration of waste-derived feedstocks aligns with circular economy goals. Future efforts focused on strain robustness and hybrid fermentation technologies could further cement role of arabitol in green industrial applications, bridging biotechnology with commercial viability (Kordowska-Wiater, 2015a; Ravikumar et al., 2022).

4.2.2. 2,3-Butanediol

2,3-Butanediol (BDO) is a versatile four-carbon diol with applications in pharmaceuticals, food, fuel additives, and chemicals. Its high energy density (27,198 J/g), which is close to that of ethanol (29,005 J/g), makes it a promising candidate for use as a rocket propellant, as demonstrated by Krueyer et al. (2021). The microbial synthesis of BDO involves key enzymes such as α -acetolactate synthase (ALS), α -acetolactate decarboxylase (ALDC), and butanediol dehydrogenase (BDH), which convert pyruvate into acetoin and subsequently into BDO (Dhodduraj et al., 2024) (Fig. 6). This pathway plays a crucial role in maintaining intracellular redox balance by regenerating NAD^+ from NADH during fermentation (Hakizimana et al., 2020; Kumar et al., 2023). However, challenges such as substrate inhibition and low production rates persist.

Fewer studies have explored the production of BDO from arabinose using various microbial systems (Table 2). For instance, *Enterobacter cloacae* NRRL B-23289 achieved a BDO yield of 0.40 g/g arabinose with a productivity of 0.63 g/L/h at an initial arabinose concentration of 50 g/L (Saha and Bothast, 1999). A recent publication from Narisetty et al. (2022) used a random mutant strain of *Enterobacter ludwigii* to demonstrate the potential of an arabinose-rich hydrolysate from dilute acid pretreated SBP to produce BDO. The fermentation was carried out using different initial substrate concentrations from 10 to 60 g/L of arabinose. The study identified the effect of substrate concentration at 60 g/L of arabinose, where the strain showed a clear sign of early-stage substrate inhibition. The highest conversion achieved was 0.43 $\text{g}_{\text{BDO}}/\text{g}_{\text{Ara}}$ (which corresponds to 86 % of the theoretical yield) with 50 g/L of initial hydrolysate arabinose concentration. While the fed-batch fermentation using both pure and SBP hydrolysate produced a higher titer of product but encountered a significant drop in yields with 0.35 and 0.31 $\text{g}_{\text{BDO}}/\text{g}_{\text{Ara}}$, respectively. The downstream processing for product recovery has been performed via an aqueous two-phase extraction system using isopropanol and $(\text{NH}_4)_2\text{SO}_4$ as solvent and electrolyte achieving about ~97 % recovery yield (Narisetty et al., 2022).

5. Galacturonic acid (GalA)

Galacturonic acid ($\text{C}_6\text{H}_{10}\text{O}_7$) is a sugar acid, an oxidized form of galactose, and one of the monomers of pectin polysaccharide. Some examples of pectin-rich feedstocks include SBP, citrus waste, apple pomace etc (Lara-Espinoza et al., 2018; Roman-Benn et al., 2023). GalA has diverse industrial applications, including its use as a gelling agent in

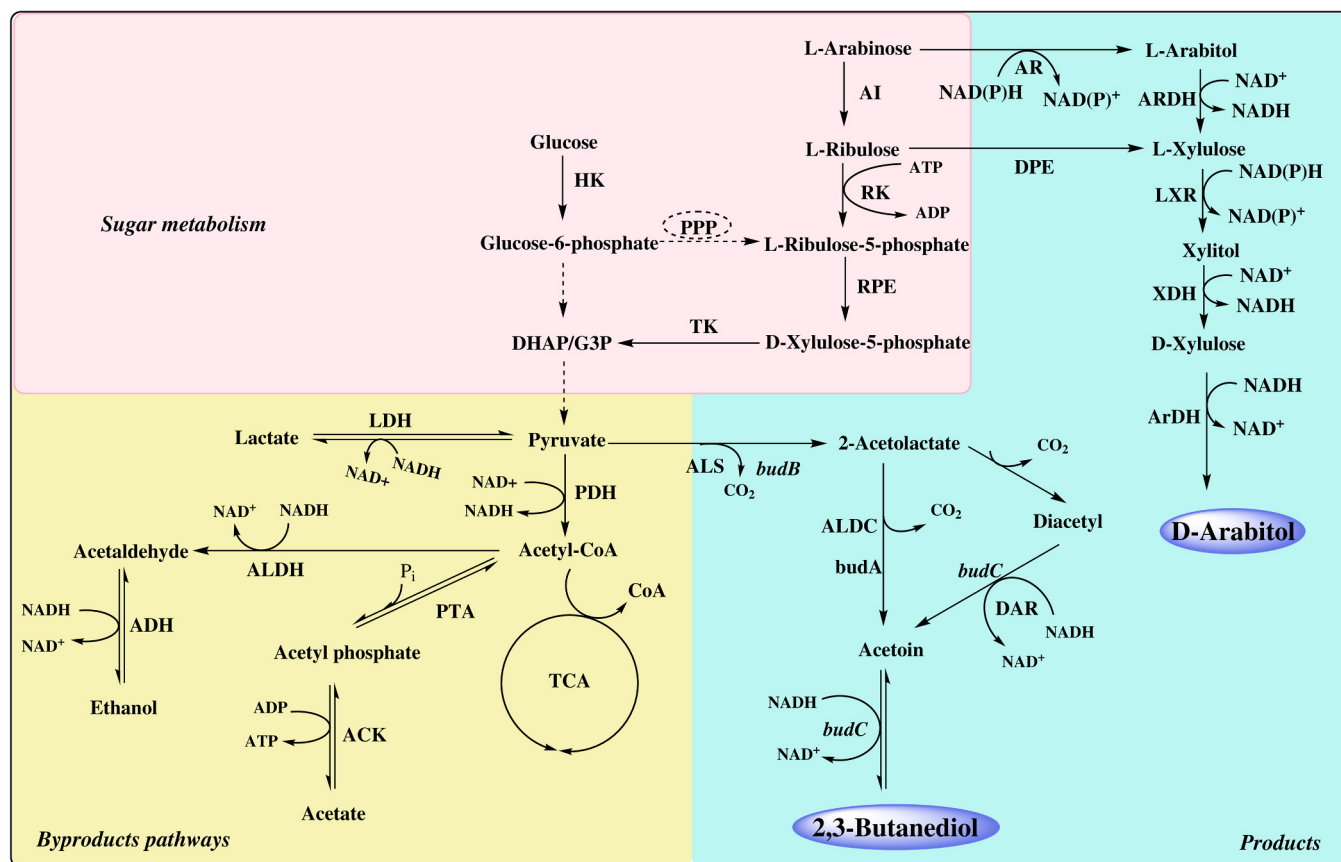


Fig. 6. Biochemical route for production of arabitol, 2,3 BDO and associated byproducts. **HK** Hexokinase; **PPP** Pentose phosphate pathway; **AI** Arabinose isomerase; **RK** Ribulokinase; **RPE** Ribulose-5-epimerase; **TK** Transketolase; **AR** Arabinose reductase; **ARDH** L-Arabitol dehydrogenase; **LXR** L-Xylulose reductase; **XDH** Xylitol dehydrogenase; **ArDH** D-Arabitol dehydrogenase; **LDH** Lactose dehydrogenase; **PDH** Pyruvate dehydrogenase; **PTA** Phosphate acetyltransferase; **ACK** Acetate kinase; **ALDH** Acetaldehyde dehydrogenase; **ADH** Alcohol dehydrogenase; **ALS** Acetolactate synthase; **ALDC** Acetolactate decarboxylase; **DAR** Diacetyl reductase; **BDH** Butanediol dehydrogenase.

the food industry, a precursor in vitamin C production, and a component in pharmaceuticals and cosmetics due to its antioxidant properties. Despite its various uses in food, pharmaceuticals, and cosmetic industries, the fermentative valorization of GalA is limited. Only a few bacteria and fungi such as *Trichoderma* sp., *Coniochaeta* sp., *Erwinia chrysanthemi*, *A. niger*, *Pseudomonas* sp., *Botrytis cinerea*, *E. coli* can naturally metabolize it (Kilgore et al., 1959; San Francisco et al., 1993; Kuorelahti et al., 2005; Richard et al., 2009). GalA metabolism in microorganisms involves complex pathways, such as the bacterial isomerase, bacterial oxidative, and the fungal reductive pathway.

5.1. Metabolic pathways for GalA utilization

5.1.1. Bacterial pathway

The bacterial isomerase pathway for GalA metabolism, found in organisms like *E. coli*, and *Bacillus subtilis* involves a series of enzymatic steps that ultimately convert D-galacturonate to central metabolic intermediates (Fig. 7). The pathway begins with the isomerization of D-galacturonate to D-tagaturonate by uronate isomerase (UxaC) (Valk et al., 2020). D-Tagaturonate is then reduced to D-altronate by D-tagaturonate reductase (UxaB), consuming one NADH molecule which follows conversion of D-altronate to 2-keto-3-deoxy-gluconate (KDG) by D-altronate dehydratase (UxaA). KDG is phosphorylated by KDG kinase (KdgK) to form 2-keto-3-deoxy-6-phosphogluconate (KDPG), consuming one ATP molecule. Finally, KDPG aldolase (KdgA) cleaves KDPG into pyruvate and glyceraldehyde-3-phosphate (G3P). This pathway is considered redox oxidative because it results in a net oxidation of NADH

to NAD⁺, with one NADH consumed in the UxaB-catalyzed step. The pathway yields two key central metabolites, one pyruvate and one G3P per galacturonate molecule, which are funneled in glycolytic pathway and can be further metabolized for energy production or biosynthesis (Richard and Hilditch, 2009). Although this pathway is not redox balanced due to the net consumption of NADH, it allows for efficient carbon flow into central metabolism. Under anaerobic conditions, bacteria may rely on additional pathways or fermentative steps to regenerate NADH, making this pathway operational under oxygen-limited environments.

Few other bacteria like *Pseudomonas* sp. and *Agrobacterium tumefaciens* follow a simpler route of GalA utilization known as bacterial direct oxidation pathway (Fig. 7) (Kilgore et al., 1959; ZAJIC, 1959). This oxidation pathway involves a single enzymatic step catalyzed by D-galacturonate dehydrogenase (UdgH). UdgH catalyzes the oxidation of D-galacturonate directly to meso-galactarate (mucic acid), using NAD⁺ as a cofactor. For each molecule of D-galacturonate oxidized, one molecule of NADH is produced. This reaction is highly exergonic, with a standard Gibbs free energy change (ΔG°) of approximately -23.8 kJ/mol. This pathway is particularly efficient in terms of enzyme economy, as it requires only one enzyme to convert D-galacturonate to a usable product. However, further metabolism of meso-galactarate typically requires oxygen, limiting the utility of this pathway under strictly anaerobic conditions. The simplicity of this pathway makes it an attractive target for metabolic engineering efforts aimed at producing meso-galactarate as a platform chemical for various industrial applications. However, the metabolism of meso-galactarate is different in

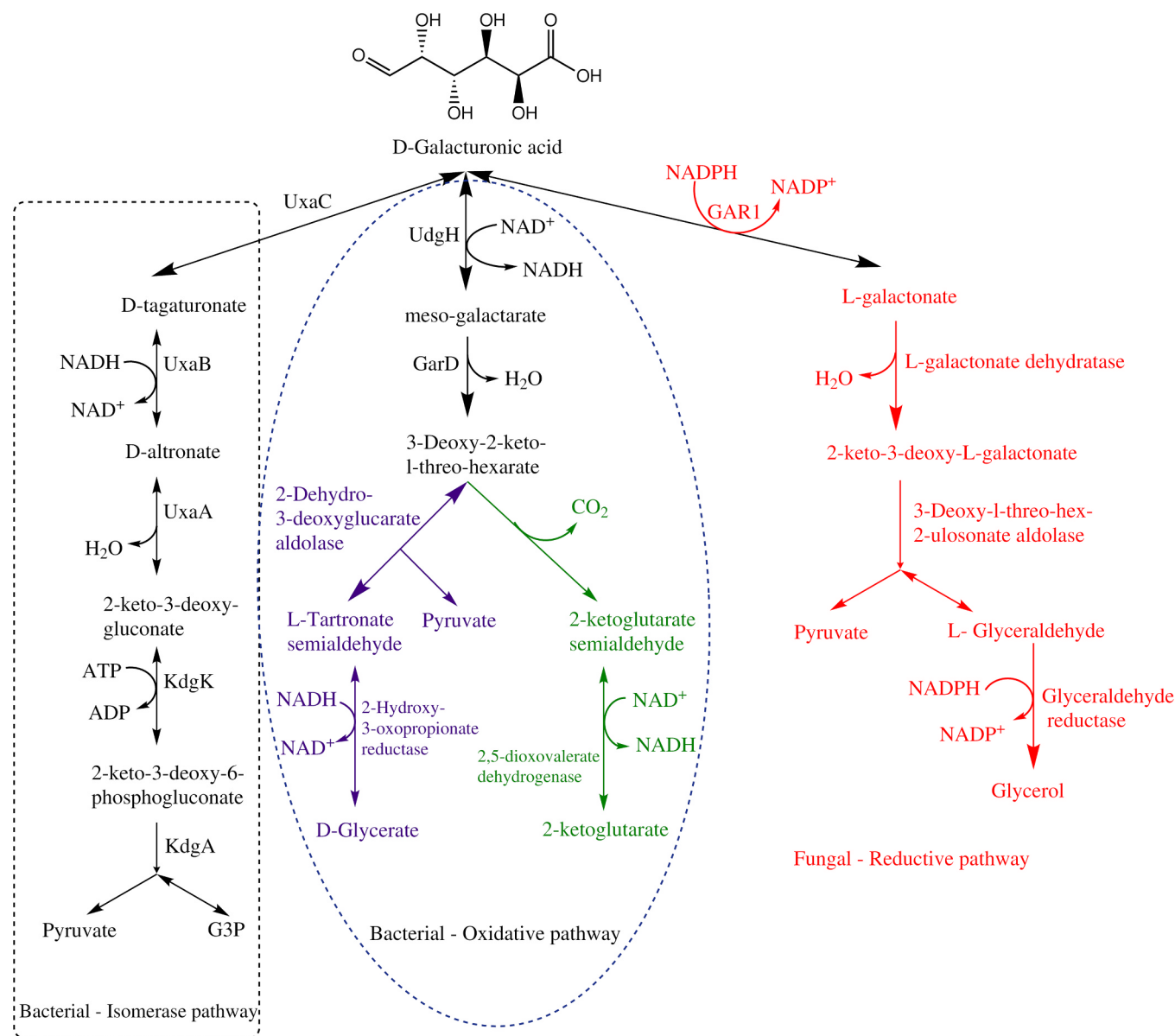


Fig. 7. Biochemical pathways for metabolism of galacturonic acid in bacterial and fungal strains. **UxC** uronate isomerase; **UxB** D-tagaturonate reductase; **UxA** D-altronate dehydratase; **KdgK** 2-keto-3-deoxy-gluconate kinase; **KdgA** 2-keto-3-deoxy-6-phosphogluconate aldose; **G3P** glyceraldehyde-3-phosphate; **UdGH** D-galacturonate dehydrogenase; **GarD** galactarate dehydratase; **GARI** D-galacturonate reductase.

different organisms such as, in *E. coli* it progresses with a dehydration reaction by galactarate dehydratase (GarD) forming 3-Deoxy-2-keto-L-threo-hexarate (Richard and Hilditch, 2009). This intermediate is split by an aldolase in formation of a pyruvate and L-tartrate semialdehyde molecules.

5.1.2. Fungal pathway

The fungal reductive pathway for GalA catabolism, prevalent in filamentous fungi like *A. niger* and *T. reesei*, comprises four enzymatic steps that convert D-galacturonate to pyruvate and glycerol (Fig. 7). The pathway begins with D-galacturonate reductase (GARI), which reduces GalA to L-galactonate using NADPH as a cofactor (Martens-Uzunova et al., 2008; Mojzita, Wiebe, et al., 2010; Vidgren et al., 2020). This initial step is both thermodynamically favored, rate-limiting, and strongly prefers NADPH over NADH (Harth et al., 2020). The enzyme exhibits a measured K_m of 4–7 mM for D-galacturonate and 30–45 μ M for NADPH in fungal systems, which denotes a relatively moderate substrate and

cofactor affinity (Kuorelahti et al., 2005; Peltonen and Richard, 2022). The strict reliance on NADPH poses a kinetic constraint, as NADPH is typically less abundant than NADH in the cell and its regeneration is not straight forward. This cofactor limitation reduces pathway flux, especially at high substrate loadings or when the pentose phosphate pathway is not highly active. Accumulation of the product L-galactonate can also inhibit GARI activity via thermodynamic feedback, and the reaction can be partially reversible depending on metabolite gradients (Kuorelahti et al., 2005; Liu et al., 2019; Peltonen and Richard, 2022). The second enzyme, L-galactonate dehydratase, cause dehydration of L-galactonate to form 2-keto-3-deoxy-L-galactonate (Mojzita, Wiebe, et al., 2010). The third step involves 2-keto-3-deoxy-L-galactonate aldolase, which cleaves its substrate into pyruvate and L-glyceraldehyde. Finally, L-glyceraldehyde reductase reduces L-glyceraldehyde to glycerol, again using NADPH as a cofactor (Kuivanen et al., 2016; Peltonen et al., 2022). This pathway is considered reductive due to the net consumption of 2-NADPH molecules per GalA processed (Biz et al., 2016). The genes

encoding these enzymes are often clustered in the fungal genome and co-regulated, allowing for efficient utilization of pectin-rich biomass. Unlike the bacterial oxidative pathway, which generate NADH that feeds into electron transport chain for ATP production, the fungal pathway follows a reductive route that consumes NADPH. Because NADPH is primarily used for biosynthetic reaction rather than catabolic steps, this pathway is less efficient in producing ATP. The unique cofactor requirement (NADPH instead of NADH) may provide an evolutionary advantage in certain ecological niches and has significant implications for metabolic engineering efforts aimed at producing value-added chemicals from pectin-rich agricultural waste using fungal hosts. The metabolic pathway for bacterial and fungi are depicted in Fig. 7.

5.2. Fermentative utilization of SBP-galacturonic acid for sustainable biochemical production

The literature on the fermentative utilization of GalA derived from SBP is extremely limited. In this section, we highlight a few distinctive studies that explore the production of ascorbic acid and its precursors, as well as mucic acid, a potential precursor for adipic acid synthesis.

5.2.1. Ascorbic acid

Ascorbic acid (AsA), also known as vitamin C or L-ascorbate, is an organic compound with the chemical formula $C_6H_8O_6$. It is a six-carbon lactone that is synthesized by plants and many animals, but not by humans, and other primates. This inability is due to a genetic mutation in the L-gulonolactone oxidase (GULO) gene, which encodes the enzyme responsible for catalyzing the last step in AsA biosynthesis (Wohlrab et al., 2020; Duque et al., 2022). AsA is a powerful antioxidant and plays crucial roles in various biological processes, including collagen synthesis, immune function, and iron absorption (Szarka and Lőrincz, 2013; Figueroa-Méndez and Rivas-Arancibia, 2015). In plants, AsA is involved in photosynthesis, growth regulation, and stress responses such as detoxifying reactive oxygen species (ROS) and stabilizing cellular mechanism under like drought and salinity (Wu et al., 2024). The GalA pathway for AsA biosynthesis is one of several routes employed by plants to produce this vital compound, particularly in fruits during ripening (Kuivanen et al., 2016). Given its diverse biological functions, AsA has found widespread applications across multiple industries. The global AsA market size was estimated at USD 1.4 billion in 2023 with compound annual growth rate (CAGR) of 8.1 % from 2023 to 2038 and is projected to reach ~ USD 2.18 billion by 2028 (Ascorbic Acid Global

Market Report, 2024). The food and beverage sector remains a significant consumer, with AsA serving as a natural antioxidant and preservative, aligning with the clean label trend (Conklin et al., 2024). The pharmaceutical industry is another major consumer, fueled by growing demand for immune-boosting supplements. In cosmetics, the ability of AsA to promote collagen synthesis has made it a popular ingredient in anti-aging products. While traditional production methods like the Reichstein process dominate, there is growing interest in alternative biosynthetic routes, particularly those utilizing pectin-rich agricultural wastes as a sustainable source of GalA, a potential precursor for AsA production.

The pathway begins with the reduction of D-GalA to L-galactonic acid, catalyzed by GAR1 (Castro et al., 2023). This enzyme was first identified in strawberry and its overexpression in *Arabidopsis* led to a 2- to 3-fold increase in whole-plant AsA content, supporting the existence and significance of this pathway. The next step is the lactonization of L-galactonic acid to L-galactono-1,4-lactone, catalyzed by the enzyme aldono-lactonase (AL) (Agius et al., 2003; Venkatesh and Park, 2014). Finally, L-galactono-1,4-lactone is oxidized to AsA by L-galactono-1,4-lactone dehydrogenase (GLDH), an enzyme localized in the inner mitochondrial membrane (Kuivanen et al., 2015) (Fig. 8). Recent advancements in metabolic engineering have demonstrated the potential of this pathway for enhancing AsA production in microorganisms. Kuivanen et al. (2015) engineered *A. niger* for the conversion of GalA to AsA by utilizing the native D-galacturonate reductase activity while deleting the gene coding for L-galactonate dehydratase. They introduced two heterologous genes from the plant AsA pathway - L-galactono-1,4-lactone lactonase from *Euglena gracilis* and L-galactono-1,4-lactone dehydrogenase from *Malpighia glabra*. This engineered strain was capable of producing AsA from pure GalA in a consolidated bioprocess, achieving product titers up to 170 mg/L (Kuivanen et al., 2015). More recently, Smirnov and Wheeler reviewed the control mechanisms of AsA biosynthesis, highlighting the critical role of GDP-L-galactose phosphorylase (GGP) in regulating AsA content (Smirnov and Wheeler, 2024). Wagner et al. (2021) demonstrated the production of L-galactonate, a key precursor in AsA biosynthesis, from SBP hydrolysate using engineered *S. cerevisiae*. The study combined enzymatic hydrolysis of pectin-rich SBP with subsequent biotransformation of the released D-GalA acid to L-galactonate. Using a strain engineered to express D-galacturonate reductase, they achieved a product concentration of 9.9 g/L L-galactonate in 48 h with a high product selectivity of 99 % (L-galactonate/D-GalA) at pH 5 using 4 % (w/v) sorbitol as a co-substrate on a synthetic media. Importantly, they demonstrated similar performance using potassium citrate buffered SBP hydrolysate, achieving a product selectivity of 97 %, marking the first direct production of L-galactonate from hydrolyzed biomass using engineered *S. cerevisiae*. The process involved a two-step approach: first, enzymatic hydrolysis of SBP using *A. niger* pectinases, which released 8.0 g/L of monomeric GalA within 48 h with a yield of 36.4 % (w/w), followed by the biotransformation step (Wagner et al., 2021).

5.2.2. Mucic acid

Mucic acid is a symmetrical sugar acid with two carboxylic groups and had a global market of 1.2 Billion USD in the year 2024 (<https://www.verifedmarketreports.com/product/mucic-acid-market/>). Environmentally benign pathways of transforming D-galacturonic acid to mucic acid are widely been explored as it serves as precursor for bioplastic production and as pharmaceutical and cosmetic ingredient. A recent landmark study by Zhang et al. (2016), where enzymatic hydrolysis of SBP released 7.8 g/L GalA, which was converted to 6.9 g/L mucic acid using an engineered *E. coli* BL21(DE3) Δ uxaC Δ garD strain. This mucic acid was subsequently transformed into adipic acid via rhenium-catalyzed deoxydehydration and platinum-catalyzed hydrogenation (Zhang et al., 2016). This study was a combination of biological and chemical catalysis which is a step towards sustainable production of adipic acid.

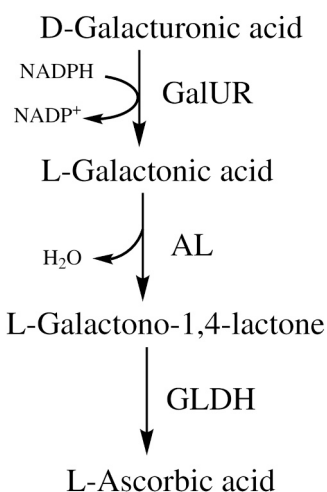


Fig. 8. Biosynthetic pathways for ascorbic acid from D-galactouronic acid. GalUR Galacturonate reductase; AL Aldono lactonase; GLDHL L-galactono-1,4-lactone dehydrogenase.

5.3. Other established applications of GalA

Gómez et al. (2016) demonstrated that POS obtained from SBP can stimulate the growth of beneficial lactic acid bacteria in a species-dependent manner, while not promoting the growth of pathogenic *E. coli* strains. In a separate study, Nadia and Nasser (2016) found that GalA itself possesses remarkable prebiotic characteristics, selectively stimulating the growth of beneficial strains such as *Lactobacillus reuteri* and *Streptococcus thermophilus* while inhibiting pathogenic bacteria (Nadia and Nasser, 2016). Beyond its prebiotic applications, GalA has shown promise in pharmaceutical uses. Noreen et al. (2017) reported that GalA-rich pectin-based materials can be used for controlled release and targeted drug delivery systems (Noreen et al., 2017; Minzanova et al., 2018). The antioxidative properties of GalA-rich pectins have also been explored, with studies showing that pectin fractions isolated from fresh vegetables possess ROS scavenging activity (Smirnov et al., 2017). Furthermore, the metal chelation properties of GalA and pectin have applications in water treatment and potentially in addressing metal deficiencies in living organisms (Minzanova et al., 2015). These diverse applications highlight the versatility of GalA as a platform molecule derived from abundant agricultural waste streams, particularly SBP, offering opportunities for sustainable production of various value-added products.

6. Glucose

6.1. Glucose-rich cellulosic hydrolysate

Glucose-rich cellulosic hydrolysates, derived from agricultural residues such as SBP, offer a sustainable and cost-effective substrate for various industrial applications. This abundance of glucose, preferred carbon source for majority of microbes, along with other monosaccharides, makes cellulosic hydrolysates an attractive feedstock for the food, pharmaceutical, and cosmetic industries. The dry basis of SBP consists of about 22–24 % of cellulosic fraction, release glucose as the primary monosaccharides upon enzymatic hydrolysis (Marzo et al., 2020; Narisetty et al., 2022). Glucose, as a sole carbon source for many microorganisms, has been extensively studied in fermentative processes, with a vast body of literature exploring its metabolism and utilization. In most microorganisms, glucose enters the cell via the phosphotransferase system (PTS) or through facilitated diffusion, followed by phosphorylation by hexokinase (Fox and Prather, 2020). It then enters glycolysis, producing pyruvate, which can be further metabolized through various pathways depending on the organism and environmental conditions. This central role in metabolism makes glucose-rich hydrolysates a valuable substrate for a wide range of industrial applications. Over the past decade, in the field of biorefinery approach, biosynthesis of numerous platform chemicals like ethanol, succinic acid, lactic acid, acetic acid, levulinic acid, and 2,5-furandicarboxylic acid has centered around the fermentative utilization of glucose in biomass hydrolysates (Takkellapati et al., 2018; Marzo et al., 2020). Glucose is a native carbon source for most industrially relevant microorganisms, which simplifies process optimization compared to non-native carbon sources like arabinose and GalA (Berłowska et al., 2016; Marzo et al., 2020).

6.2. Fermentative utilization of SBP-glucose for sustainable biochemical production

Extensive research exists on glucose-based fermentation for biosynthesis of high-value products. This section highlights the utilization of glucose from SBP for the synthesis of various chemicals. One such recent study by Marzo et al. (2021) investigated the valorization of fungal hydrolysates of SBP for lactic acid production. The researchers used solid-state fermentation with fungi to produce hydrolytic enzymes for SBP hydrolysis. Out of two strains used, they found *Lactobacillus plantarum* outperformed *Lactobacillus casei* for lactic acid production,

yielding 34 % higher concentrations with a maximum lactic acid concentration of 30 g/L (Díaz et al., 2020; Marzo et al., 2021). Using *Bacillus coagulans* A166 in a continuous fermentation process with cell retention, De Oliveira et al. (2020) achieved a maximum lactic acid concentration of 31.7 g/L and a yield of 0.71 g/g. It is reported that 2781.0 g of lactic acid was produced using 3916.9 g of sugars from hydrolyzed SBP, with a maximum productivity of 18.1 g/L/h. The study also demonstrated the feasibility of integrating lactic acid production into existing SB processing facilities, potentially improving the economic viability of the sugar industry (De Oliveira et al., 2020). A recent study investigated the feasibility of production of succinic acid using SBP hydrolysate, the process begins with the efficient fractionation of SBP into pectins, phenolic compounds, and sugar-rich hydrolysate. This hydrolysate, rich in glucose and arabinose, served as a fermentation feedstock for producing succinic acid using the bacterium *Actinobacillus succinogenes*. The fermentation achieved a succinic acid concentration of 30 g/L, with a productivity of 0.62 g/L/h and a yield of 0.8 g/g and from 1 kg of SBP, 268 g of succinic acid was accumulated (Alexandri et al., 2019b). A recent study by Patelski et al. (2024) reported that a maximum yield of 5.38 ± 0.11 kg of ethanol per 100 kg of SBP was achieved by combining microbial hydrolysis with fermentation technology. The research focused on using the fungus *Trichoderma viride* for cellulase hydrolysis of SBP followed by utilizing the released sugars for bioethanol production (Patelski et al., 2024). Ghanem (1992) used a mixed culture of *Trichoderma reesei* and *Kluyveromyces marxianus* for single cell protein production from SBP, achieving a protein yield of 54 % with an efficiency of 42 % in converting SBP to proteins (Ghanem, 1992). Few other examples include, production of poly(3-hydroxybutyrate) (PHB), a type of PHA, using SBP-derived glucose using *Haloarcula* sp. TG1, achieving a PHA content of 45.6 % of the biomass (Marzo-Gago et al., 2023). Additionally, based on the study by Emrah Alkaya and Goksel N. Demirel, SBP can be effectively used to produce volatile fatty acids (VFAs) through anaerobic acidification. The main VFAs produced were acetic, propionic, and butyric acids, with smaller amounts of valeric acid (Alkaya et al., 2011). In addition to the aforementioned applications, SBP has also been used as a substrate for the production of several enzymes with significant industrial relevance, including cellulase, xylanase, polygalacturonase, dextranase, and arabinanase, as shown in Table 3.

7. Challenges associated with biovalorization of SBP

7.1. Proper pretreatment technique

The pretreatment of SBP for extraction of fermentable sugars for valorization into biofuels, biochemicals or bioplastics faces significant challenges that often undermine its sustainability goals. While SBP is a promising renewable feedstock rich in cellulose, hemicellulose, and pectin, current pretreatment methods frequently rely on energy-intensive processes or harsh chemicals, creating paradoxical trade-offs between resource efficiency and environmental impact. A primary issue lies within the widespread use of thermochemical pretreatments involving acids and alkaline agents. For instance, sulfuric acid pretreatment increases the cellulose accessibility by solubilizing hemicellulosic fraction but generates inhibitors like HMF and furfural by sugar degradation, which necessitates expensive detoxification prior to fermentation (Kühnel et al., 2011; Marzo et al., 2021). Lime pretreatment for lignin removal, though less toxic, requires high loadings (0.4 g lime/g SBP) and prolonged incubation (36 h), raising energy demands despite operating at moderate temperatures (40 °C) (Dredge et al., 2011). Such methods risk neutralizing the environmental benefits of using agricultural waste by introducing chemical waste streams and carbon-intensive processing steps.

The economic viability of these approaches is further strained by scalability challenges. Enzymatic hydrolysis, a greener alternative, depends heavily on effective pretreatment to break down lignocellulosic structures. However, enzymatic cocktails are expensive often exceeding

Table 3
Enzymes produced using SBP as substrate.

Enzyme	Microorganism	Genotype	Activity	Conditions used	Enzyme application	Reference
Cellulase	<i>Aspergillus fumigatus</i> NRC-122	UV mutant	4.6 FPU/ml	SSF	Saccharification of cellulose-rich biomass; textile processing; laundry detergents	Fadel et al. (2021)
	<i>Trichoderma reesei</i>	Wildtype	0.46 FPU/ml	SSF		Moosavi-Nasab and Majidi-Nasab (2010)
Xylanase	<i>Aspergillus awamori</i> 2B.361	Mutant	1.9 ± 0.2 FPUase/g _{SBP}	SSF	Degradation of hemicelluloses to xylose, paper bleaching, increased digestibility in animal feed, baking industry	Marzo et al. (2020)
	<i>Aspergillus awamori</i> 2B.361	Mutant	24.6 ± 0.6 U/g _{SBP}	SSF		Marzo et al. (2020)
	<i>Aspergillus awamori</i> 2B.361	Mutant	9.3 ± 1.1 U/g _{SBP}	SSF		Marzo et al. (2020)
Exo-polygalacturonase	<i>Aspergillus awamori</i> NRC-F18	Wildtype	396.4 U/g _{SBP}	SSF	Pectin breakdown for fruit juice clarification, vegetable oil extraction, textile processing	Roshdy et al. (2020)
Polygalacturonase	<i>Aspergillus sojae</i> ATCC 20235	Wildtype	909.5 U/g _{SBP}	SSF	Pectin removal for juice and wine clarification, degumming plant fibers	Roshdy et al. (2020)
Dextranase	<i>Bacillus gibsonii</i> S-2	Wildtype	3600 U/g _{SBP}	SSF	Degradation of dextran during sugar making; dental care for plaque prevention; food industry as sugar modifier; supplement for blood plasma	Li et al. (2005)
	<i>Aspergillus awamori</i> F-234	Wildtype	1057 U/g _{SBP}	SSF		Mouafi et al. (2016)
Exo-arabinanase	<i>Fusarium oxysporum</i>	Wildtype	0.25 u/ml	SmF	Hydrolysis of arabinan to arabinose, prebiotic production (AOS), preventing haze formation in fruit and vegetable juices	Chellas et al. (2000)

20 % of total production costs, and their efficiency remains limited without prior chemical or energy-intensive physical disruption of SBP which corresponds to ~15–30 % of process energy (Liu et al., 2016; Bhardwaj et al., 2021; Marzo-Gago et al., 2023). In that context, steam explosion and dilute acid methods generate liquid fractions requiring pH adjustment, increasing salt loads and downstream processing complexity (Mussatto, 2016; De Oliveira et al., 2020; Gönen et al., 2023).

Emerging biological pretreatments using microbes or enzymes offer partial solutions but face technical hurdles. Fungal pretreatment, for instance, reduces inhibitor formation but operates slowly (days to weeks) and struggles with substrate specificity (Marzo et al., 2021). Alkaline hydrogen peroxide (AHP) pretreatment avoids harsh acids but demands large oxidant volumes, raising concerns about oxygen radical byproducts and process safety (Marzo et al., 2021). Even advanced methods like high-voltage electrical discharge (HVED), which enhance pectin extraction, remain energy-intensive and confined to lab-scale applications (Almohammed et al., 2017).

Overall, while various pretreatment strategies for SBP have demonstrated potential in specific contexts, no single method currently offers a complete solution that balances efficiency, cost, and environmental performance. A paradigm shift is needed, either through the development of novel, low-energy pretreatment technologies or the integration of synergistic processes to fully unlock the value of SBP in a commercially viable and sustainable manner.

7.2. Arabinose utilization constrains

L-Arabinose constituting a major portion of SBP presents significant challenges for its efficient bioconversion into value-added products. Despite its abundance, the utilization of arabinose has been largely overlooked in industrial biotechnology compared to hexoses like glucose. One of the primary issues is the limited number of potential microorganisms capable of metabolizing it efficiently. For example, the proven industrial strain *S. cerevisiae* lacks native pathways for arabinose catabolism. Although metabolic engineering strategies have enabled the introduction of bacterial and fungal arabinose pathway into *S. cerevisiae*, the efficiency of these engineered strains remains suboptimal due to poor uptake rate, slow metabolic flux through the introduced pathways and cofactor imbalance (Becker and Boles, 2003; Richard et al., 2003; Wiedemann and Boles, 2008). A major limitation in arabinose fermentation is transport inefficiency. Unlike glucose, which has dedicated high-affinity transporters, arabinose uptake in yeast relies on non-specific, low-affinity transporters, leading to slow sugar uptake and prolonged lag phases (Subtil et al., 2011). Even when arabinose is taken up, its metabolic conversion remains inefficient due to enzymatic bottlenecks. The pathway involves multiple enzymatic steps, which together convert arabinose into intermediates that enter the pentose phosphate pathway and central carbon metabolism. These steps are slower compared to glycolysis, leading to reduced carbon flux and lower overall productivity. In bacterial systems, arabinose utilization is tightly regulated by CRP as part of carbon catabolite repression. Glucose availability dictates sugar preference, with low glucose concentrations triggering the utilization of secondary sugars like arabinose. Consequently, this hierarchical sugar preference often results in delayed arabinose utilization in mixed-sugar environments, limiting its industrial application (Fox and Prather, 2020). Beyond microbial constraints, process engineering challenges also hinder industrial arabinose fermentation. Most available arabinose-rich feedstocks require extensive pretreatment and often generate inhibitory compounds like furfural, HMF, and phenolics, which negatively impact microbial growth and fermentation performance (Lavarack et al., 2002; Narisetty et al., 2022).

To address these challenges, various strategies have been explored, including the engineering of more efficient arabinose transporters, modification of CCR pathways to enable co-utilization of glucose and

arabinose, and optimization of metabolic flux to improve carbon conversion efficiency. Adaptive laboratory evolution and genome-scale metabolic modeling have also been used to improve arabinose fermentation performance, but further advancements are needed to make it competitive with glucose fermentation. While arabinose holds promise as a renewable feedstock, overcoming these limitations remains a key challenge in making its bioconversion industrially feasible (Wiedemann and Boles, 2008; Kim et al., 2015; Sievert et al., 2017; Fox and Prather, 2020).

7.3. Galacturonic acid utilization constrains

GalA being a significant component in the pectin rich from diverse feedstocks like SBP, citrus peel, apple pomace, poses major challenges in microbial fermentation process. The acidic nature of GalA ($pK_a = 3.51$) creates the first line of complication, as fermentation media derived from pectin rich materials equilibrate at pH levels where the undissociated form predominates. This form exerts strong inhibitory effects on cell metabolism and negatively impacting any mixed sugar fermentation by inhibiting sugar intake. Most of the industrially relevant organisms lack the metabolic network for metabolizing GalA. Even when metabolic engineering introduces heterologous pathways for GalA catabolism, fundamental challenges persist, including glucose-mediated repression of alternative sugar uptake systems and cofactor imbalances (Protzko et al., 2018). Recent attempts to address these limitations through transporter engineering (e.g., *GatA* expression) and co-utilization strategies have shown partial success. Even engineered strains face persistent hurdles: heterologous pathways for GalA catabolism, such as the *A. niger*-derived reductive pathway, suffer from cofactor imbalances due to NADPH dependency, necessitating auxiliary systems like sorbitol dehydrogenases to regenerate reducing equivalents (Harth et al., 2020; Wagner et al., 2021). Byproduct formation introduces additional complications. Glycerol accumulation in fungal pathway, a consequence of NADPH reoxidation during GalA reduction, diverts carbon away from target products. Even in alternative microbial hosts like *Lactobacillus suebicus*, which natively ferments GalA to acetate and lactate, low biomass yields (0.09 g/gGalA) and mixed-acid profiles limit commercial viability (Valk et al., 2020). Emerging solutions face their own limitations: transporter engineering improves substrate uptake but fails to eliminate glucose-mediated repression, while dynamic pathway regulation remains experimentally challenging. These intertwined challenges ranging from fundamental microbial physiology to process engineering constraints, highlight the need for integrated approaches combining acid-tolerant chassis development, cofactor-balanced pathway design, and transporter systems decoupled from native regulatory networks.

7.4. Supply chain, logistics, and cost effectiveness

SBP presents both supply chain and cost-related limitations as a biorefinery feedstock for platform chemicals. A primary supply chain challenge is its seasonally dependent availability, as SB processing occurs cyclically, leading to feedstock inconsistency and necessitating costly storage solutions to prevent spoilage (Kawa-Rygielska et al., 2013). Additionally, wet SBP's high water content makes it bulky and expensive to transport over long distances, leading to inefficiencies in logistics and higher transportation expenses (Kolfshoten et al., 2014). Storage and preservation also pose challenges, as SBP deteriorates quickly due to its high moisture content and susceptibility to microbial spoilage. Energy-intensive drying or ensiling processes are often required to maintain feedstock quality, further adding to operational costs.

Geographically, SBP availability is restricted to regions with established SB-based sugar industries, limiting scalability. From a cost perspective, while SBP is cheaper (~\$ 80 – 120/ton on dry basis) (Beet pulp Market Prices, 2025; García-Velásquez and van der Meer, 2023)

than commercial glucose (\$400–600 /ton) (Dextrose Prices, Monitor, 2025), its valorization requires energy- and resource-intensive pretreatments and enzymes, which account for 20–30 % of total production costs (Agrawal et al., 2021; Beig et al., 2021). Despite these limitations, SBP's cost-effectiveness stems from its low initial feedstock cost and potential integration into circular economy models. Colocation of biorefinery with sugar factories could reduce transportation and pretreatment overheads, while valorizing a waste product offsets disposal costs and aligns with sustainability incentives (Kolfshoten et al., 2014). Thus, while SBP biorefineries face economic and logistical barriers, addressing these challenges through strategic optimization of supply chain logistics, energy-efficient pretreatment technologies, and cost-effective enzyme utilization could significantly enhance their economic viability. By integrating innovative solutions such as enzyme recycling, decentralized processing models, and advanced storage systems, SBP biorefineries can reduce production costs and improve resource efficiency. These advancements would not only make SBP-based systems more competitive with conventional pure sugar-based platforms but also contribute to the development of sustainable and circular bioeconomy.

8. Conclusion & future perspectives

SBP, a major by-product of the sugar industry, holds considerable promise as a renewable and abundant feedstock for the production of high value bio renewables. The valorisation of SBP not only enhances the economic viability of the sugar industry but also aligns with broader sustainability goals, including waste minimization, resource efficiency & circularity, and the advancement of a circular bioeconomy. Continued research and technological development in this domain are critical to fully unlocking the potential of SBP. This review has outlined the compositional complexity of SBP and explored a range of fractionation and bioconversion strategies, with a particular focus on the recovery and utilization of the less explored sugars including arabinose and GalA which stand out as particularly promising avenues. These components offer unique opportunities as substrates for the development of advanced metabolic pathways and novel bioproducts.

Looking forward, the future of SBP valorisation lies in integrating emerging fractionation technologies with state-of-the-art metabolic engineering. Innovative solvent systems such as deep eutectic solvents and ionic liquids hold potential for enhancing the selective separation of SBP constituents, enabling more efficient downstream microbial fermentation. Simultaneously, advances in synthetic biology and genome editing—especially CRISPR-Cas9—are accelerating the development of microbial strains capable of efficiently co-fermenting multiple SBP-derived sugars, including glucose, arabinose, and GalA. Strategic engineering of metabolic pathways may enable the biosynthesis of rare and valuable compounds. For instance, targeted engineering of the arabinose metabolic pathway in microbial hosts may enable the biosynthesis of rare sugars such as L-gluco-heptulose, a compound with emerging potential in cancer therapeutics. Likewise, optimizing GalA metabolism could enhance the microbial production of key intermediates for AsA synthesis. Moreover, the design of consolidated bioprocessing platforms, wherein single microbial strains are capable of both polysaccharide hydrolysis and fermentation, could significantly simplify SBP biorefinery processes and improve overall economic feasibility.

In the coming years, the convergence of advanced metabolic engineering tools, process intensification, and artificial intelligence-based optimization is expected to transform SBP from a low-value residue into a key feedstock for the next generation of biomanufacturing. These innovations position SBP valorisation as a model for integrating biotechnology with circular economy principles, offering both commercial and environmental benefits.

CRedit authorship contribution statement

Venkatesh Balan: Writing – review & editing. Vinod Kumar:

Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Conceptualization. **Deepti Agrawal:** Writing – review & editing, Writing – original draft, Conceptualization. **Sunil K Maity:** Writing – review & editing. **Kawinharsun Dhodduraj:** Writing – review & editing, Writing – original draft, Software, Conceptualization. **Roberto Parra Saldivar:** Writing – review & editing, Conceptualization. **Frederic Coulon:** Writing – review & editing, Conceptualization. **Vivek Narisetty:** Writing – review & editing, Conceptualization. **Sayed Ali Nabavi:** Writing – review & editing, Conceptualization.

Declaration of Competing Interest

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

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Data availability

No data was used for the research described in the article.

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Beets beyond sugar: potential and limitations of sugar beet pulp as a feedstock for biorefineries

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