

Review

Valorization of Agricultural Byproducts into Bacterial Cellulose via Kombucha Symbiotic Consortia: A Review on the ‘Feedstock–Strain–Property–Application’ Paradigm

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ABSTRACT: Bacterial cellulose is a class of sustainable biopolysaccharides with a three-dimensional nanofiber network structure. Owing to its high chemical purity, excellent mechanical properties, and good biocompatibility, it has broad application prospects in biomedicine, active packaging, and flexible electronics. The high economic and environmental costs of traditional synthetic culture media represent a key bottleneck limiting their industrial-scale production. By leveraging the metabolic synergy of the Symbiotic Culture of Bacteria and Yeast (SCOBY), agricultural byproducts such as molasses, tea waste, and crop straw can be converted into high-value bacterial cellulose, providing a viable pathway for low-carbon, green biomanufacturing. This paper establishes a systematic research paradigm of “feedstock–strain–property–application” and comprehensively reviews research progress on the production of bacterial cellulose from agricultural byproducts via kombucha fermentation: it elucidates the metabolic symbiosis patterns of yeast, *Acetobacter*, and lactic acid bacteria in the kombucha symbiotic culture, as well as the molecular regulatory mechanisms of the *bcs operon* and the second messenger c-di-GMP in cellulose biosynthesis; it analyzes the chemical composition characteristics of typical agricultural byproducts, revealing the regulatory roles of carbohydrates, nitrogen sources, minerals, and phenolic compounds in the substrates on microbial community structure, bacterial cellulose yield, as well as the material’s microstructure, crystallinity, and thermomechanical properties, and clarifies that endogenous active components in waste materials can enable *in-situ* functionalization of bacterial cellulose; summarize technical strategies for screening high-yield strains, rational optimization of symbiotic microbial communities, and genetic engineering modifications; introduce a closed-loop biorefining model for the high-value utilization of all fermentation components, as well as diverse application scenarios for functionalized bacterial cellulose. This review provides a systematic theoretical reference on the utilization

of agricultural waste as a resource and the large-scale production of low-cost, high-performance bacterial cellulose, thereby contributing to the development of green biomanufacturing within the context of a circular bioeconomy.

Keywords: Bacterial cellulose; Kombucha symbiotic consortia; Agricultural byproducts; Microbial breeding; Strain-property relationships; Circular bioeconomy

1. Introduction

The global processing of industrial crops generates massive amounts of lignocellulosic byproducts, including a wide variety of biomass resources such as sugarcane bagasse [1], tea waste [2], fruit pomace, molasses [3], and corn cobs. Currently, most of this waste is disposed of through incineration or landfilling, which not only exacerbates environmental pollution and incurs high disposal costs but also results in a significant waste of biopolymers and nutritional resources [4–6].

At the same time, global market demand for renewable, biodegradable, bio-based materials continues to grow [7]; however, nature can synthesize 100–150 billion metric tons of cellulose annually to meet this growing demand [8,9], traditional plant-based cellulose relies primarily on cotton and wood supplies, which are increasingly constrained by land competition, water scarcity, pollution from chemical processing, and deforestation [10], creating an urgent need to develop high-performance biopolymer alternatives and efficient, green biomanufacturing processes [11,12].

Bacterial cellulose (BC) is an extracellular β -1,4-glucan primarily synthesized by microorganisms of the genus *Komagataeibacter* [13]. Compared to plant cellulose, bacterial cellulose is naturally free of lignin, hemicellulose, and pectin, and possesses extremely high chemical purity; its unique biosynthetic pathway allows it to assemble into a three-dimensional network structure of ultrafine nanofibers with diameters ranging from 20 to 100 nm, endowing the material with a water-holding capacity exceeding 100 times its own weight, a Young's modulus of 15–35 GPa, a crystallinity of over 80%, and excellent biocompatibility [14–17]. It holds broad application prospects in fields such as biomedicine, active packaging, and flexible electronics, making it a highly competitive alternative to plant-based cellulose [18]. However, the high cost of raw materials for traditional synthetic culture media, such as the Hestrin-Schramm (HS) medium, has consistently been a key obstacle to the large-scale industrial production of bacterial cellulose [19,20].

Kombucha fermentation provides an integrated biorefining platform for low-cost, sustainable bacterial cellulose production. This system relies on the metabolic synergy of a SCOBY and can directly use abundant agricultural byproducts as fermentation substrates in place of expensive analytically pure reagents [21–23], significantly reducing raw material costs; Bioactive components such as polyphenols and organic acids naturally present in fermentation byproducts can be incorporated into the cellulose matrix *in situ*, endowing the material with intrinsic antioxidant and antibacterial properties without the need for exogenous additives; fermentation wastewater can also be recycled or further processed for value-added applications, enabling a near-zero-waste production model and establishing a viable technical framework for the circular bioeconomy [23,24].

In recent years, several reviews have summarized alternative substrate systems for bacterial cellulose [14,25] or industrial application scenarios [20,26]; however, most of these studies have remained at the level of a static listing of raw materials and have failed to establish a multiscale, systematic correlation between the chemical composition of upstream raw materials, microbial community metabolic regulation, and the performance of downstream materials. To address this research gap, this paper constructs a unified “Feedstock–Strain–Property–Application” (FSPA) analytical paradigm. Using the kombucha symbiotic microbial community as the core carrier, this study systematically elucidates research progress in the high-

value utilization of agricultural byproducts for bacterial cellulose production: First, it analyzes the metabolic symbiosis mechanisms of the SCOBY microbial community and the molecular regulatory basis of bacterial cellulose synthesis; second, we categorize and evaluate the chemical characteristics of typical agricultural byproducts, elucidating the regulatory patterns by which substrate composition influences microbial community structure, cellulose yield, and the physicochemical properties of the material; next, we summarize the technical approaches for screening high-yield strains, optimizing symbiotic microbial communities, and genetic engineering modifications; finally, we introduce a circular production model for the high-value utilization of all fermentation components, as well as application scenarios for waste-derived functionalized bacterial cellulose. This paper aims to provide a systematic theoretical framework and technical roadmap for the low-cost, large-scale production of high-performance bacterial cellulose from agricultural byproducts, thereby promoting its industrial implementation within a circular bioeconomy system (see Figure 1).

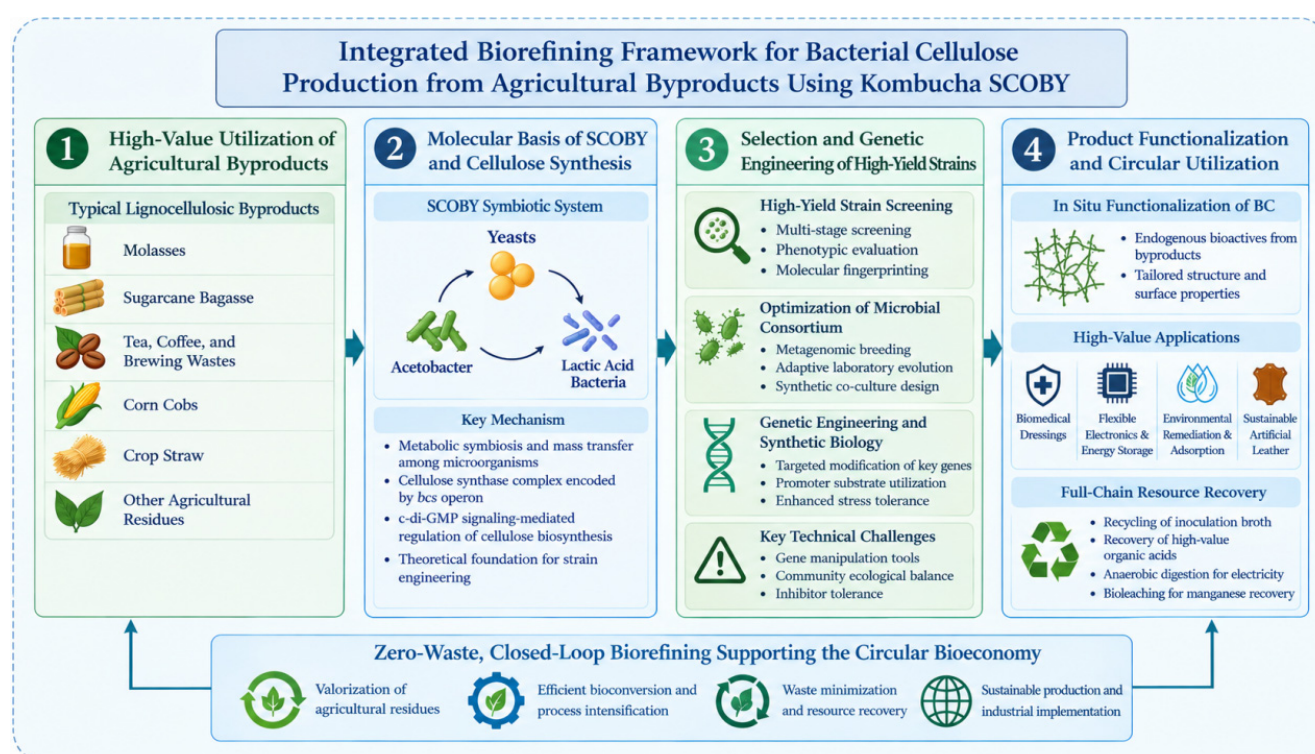


Figure 1. Integrated biorefining framework for bacterial cellulose production from agricultural byproducts using the Kombucha symbiotic culture (SCOBY). The framework integrates four interconnected research dimensions: (1) high-value utilization of agricultural byproducts as low-cost substrates for bacterial cellulose (BC) production; (2) the molecular basis of SCOBY-mediated microbial symbiosis and cellulose biosynthesis, including microbial interactions, the *bcs* operon, and c-di-GMP signaling; (3) screening, consortium optimization, and genetic engineering of high-yield strains to improve cellulose productivity, substrate utilization, and stress tolerance; and (4) *in situ* BC functionalization, high-value applications, and full-chain resource recovery. These strategies collectively establish a zero-waste, closed-loop biorefining pathway that couples agricultural-residue valorization with efficient bioconversion, product diversification, waste minimization, and resource recovery, thereby supporting the development of a sustainable circular bioeconomy.

2. SCOBY as a Natural Bioreactor for Bacterial Cellulose Synthesis

The SCOBY is a sophisticated, gel-like biofilm comprising a dense cellulose matrix interwoven with taxonomically diverse communities of acetic acid bacteria (AAB) and yeasts [27]. During the fermentation of kombucha, the SCOBY assembles as a pellicle at the gas–liquid interface, which essentially constitutes the synthesized BC membrane [28]. AAB, particularly species such as *Komagataeibacter xylinus*, *K.*

hansenii, *K. rhaeticus*, and *K. intermedius*, serve as the primary biosynthetic engines for this cellulosic scaffold [29,30].

2.1. Effects of Metabolic Interactions Among Microorganisms on BC Synthesis

Throughout the fermentation process, three types of microorganisms maintain a highly synergistic metabolic symbiotic relationship (see Figure 2 for metabolic pathways). The entire conversion process is as follows: yeast converts carbon sources such as sucrose into ethanol and carbon dioxide through glycolysis, while simultaneously producing various organic acids and vitamins [31]; *Acetobacter* primarily oxidizes glucose via the pentose phosphate pathway (HMP) to generate byproducts such as gluconic acid, while also oxidizing ethanol to produce acetic acid. These processes not only provide energy (ATP) for cell growth but also supply the key precursor uridine diphosphoglucose (UDP-Glc) for bacterial cellulose synthesis, ultimately leading to the synthesis and secretion of nanoscale cellulose fibers that form a gel-like symbiotic bacterial membrane [31,32]. Lactic acid bacteria, on the other hand, produce lactic acid through homofermentative or heterofermentative fermentation, lowering the pH of the fermentation system and creating a unique acidic environment that inhibits the growth of contaminating microorganisms; at the same time, they can indirectly regulate the yield and properties of bacterial cellulose by influencing community metabolic flux [33,34].

2.2. Cellulose Synthesis Genes and Regulatory Networks

The biosynthesis of bacterial cellulose is precisely regulated by an enzyme system encoded by specific gene clusters, using UDP-Glc as the starting precursor. This precursor is also involved in the synthesis of cutin polysaccharides in organisms such as plants, reflecting the evolutionary conservation and functional overlap of biosynthetic pathways [35].

In cellulose-producing strains such as *Komagataeibacter xylinus*, the cell-membrane-localized cellulose synthase complex uses UDP-Glc as a substrate to catalyze the polymerization of glucose monomers into glucan chains linked by β -1,4-glycosidic bonds. The *bcs operon* primarily encodes this complex: *BcsA* serves as the core catalytic subunit, carrying out the glycosyltransferase reaction; *BcsB* serves as the regulatory subunit, working in concert with *BcsA* to facilitate the polymerization of the sugar chains and their transmembrane secretion [36]. After being secreted into the extracellular space, the glucan chains are further assembled into microfibrils, ultimately forming a three-dimensional nanonetwork structure known as bacterial cellulose. Elucidating the structure and function of the synthetic pathway and key enzyme complexes provides the molecular basis for using genetic engineering to specifically optimize yield and regulate fiber properties [37].

Currently, the functional division of the *bcsABCD* gene cluster in *Komagataeibacter* has been fully elucidated: *BcsA* contains the catalytic active site and directly mediates the polymerization of UDP-Glc; *BcsB* participates in substrate recognition and binding; *BcsC* acts as a channel protein to facilitate the passage of sugar chains through the outer membrane; and *BcsD* regulates the crystallization process and oriented arrangement of microfibrils [38]. Pan-genomic analyses of the genera *Komagataeibacter* and *Novacetimonas* further reveal that the *bcs operon* exhibits rich sequence polymorphism and evolutionary divergence, serving as the core genetic factor underlying differences in cellulose yield and material properties among different strains [39].

Furthermore, the second messenger cyclic di-guanosine monophosphate (c-di-GMP) is a key signaling molecule regulating cellulose synthesis; its intracellular concentration precisely controls cellulose synthesis efficiency by influencing *BcsA* activity [40]. Systematic analyses of the synthetic pathway, the function of the *bcs operon*, and the regulatory network have laid the theoretical foundation for synthetic biology-based

engineering: by knocking out or overexpressing specific genes, it is possible to selectively increase yield, regulate fiber diameter and crystallinity, or confer new functional properties on bacterial cellulose [37,41].

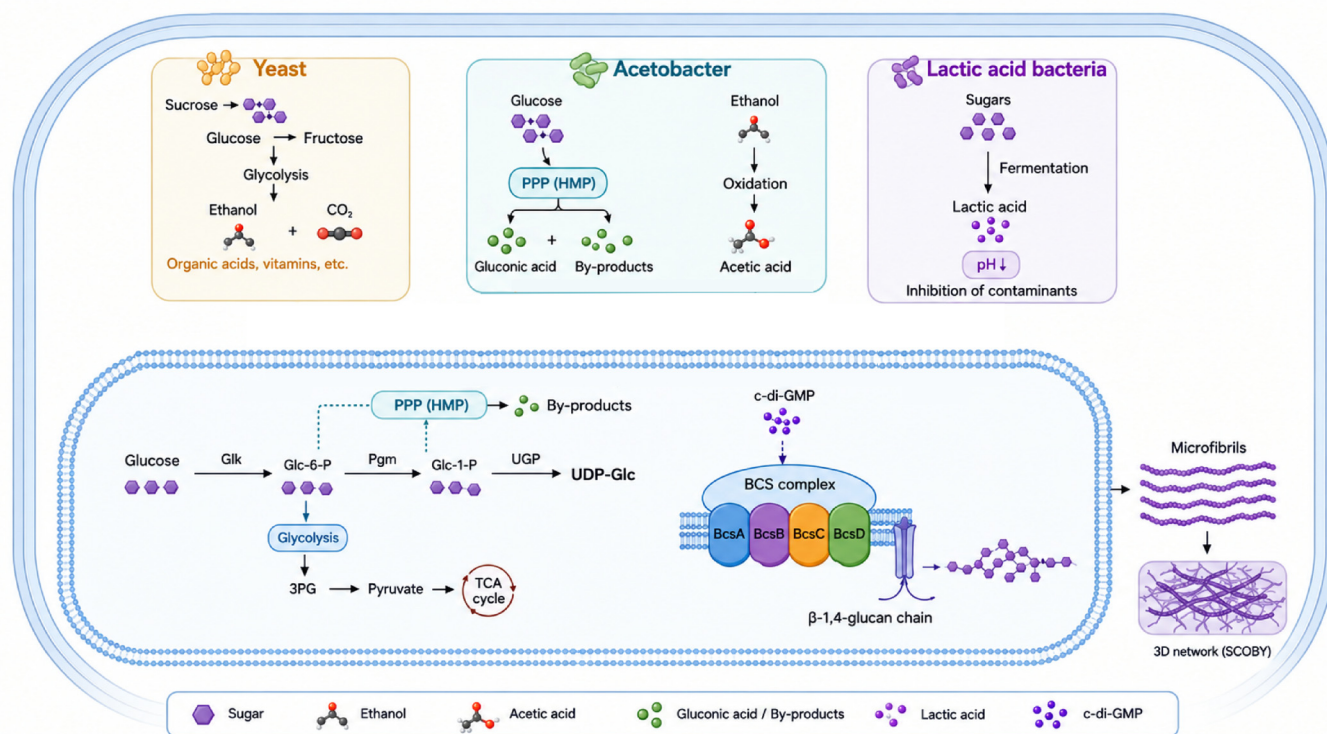


Figure 2. Metabolic interactions within the kombucha symbiotic microbial consortium and their contribution to bacterial cellulose biosynthesis. Yeasts hydrolyze and metabolize sugars, converting sucrose into glucose and fructose and subsequently producing ethanol, carbon dioxide (CO₂), and other metabolites through glycolysis. Acetobacter utilizes glucose through central metabolic pathways, including the pentose phosphate pathway (PPP/HMP), generating gluconic acid and other metabolites, while ethanol is oxidized to acetic acid. Lactic acid bacteria ferment available sugars to produce lactic acid, thereby contributing to the acidification of the fermentation environment. Within bacterial cellulose-producing acetic acid bacteria, glucose is converted through the sequential formation of glucose-6-phosphate (Glc-6-P), glucose-1-phosphate (Glc-1-P), and uridine diphosphate glucose (UDP-Glc), which serves as the direct precursor for cellulose synthesis. The bacterial cellulose synthase (BCS) complex, comprising the core components *BcsA*, *BcsB*, *BcsC*, and *BcsD*, polymerizes UDP-Glc into β-1,4-glucan chains, while intracellular c-di-GMP acts as a key regulatory signal associated with cellulose synthase activation. The newly synthesized glucan chains are subsequently exported and assembled into extracellular microfibrils, ultimately forming the three-dimensional nanofibrillar network characteristic of the SCOBY-associated bacterial cellulose matrix.

3. Valorization of Industrial Crop Byproducts as Sustainable Feedstocks

Traditionally, black tea and sucrose have served as the standard nitrogen and carbon sources for kombucha fermentation [42,43]. Recently, the strategic transition toward utilizing industrial crop byproducts as low-cost, sustainable alternatives has emerged as a focal point in BC research. This section systematically evaluates the chemical profiles of various agricultural residues and their decisive impact on BC yield, macromolecular assembly, crystallinity, and thermo-mechanical properties. Evidence suggests that specific waste streams not only drastically reduce production costs but also surpass conventional HS media in yield and material performance. Furthermore, techno-economic insights underscore the dual economic and environmental dividends of substituting refined reagents with these renewable residues.

3.1. Industrial Crop Byproducts for Cost-Effective BC Synthesis

Globally, billions of metric tons of agricultural residues—such as sugarcane bagasse, corn cobs, rice husks, fruit peels, distillers' grains, and whey—are generated annually. If not properly managed, these

materials not only result in a waste of resources but also exacerbate environmental pollution [22,44]. Converting such waste into high-value-added bacterial cellulose aligns with the principles of a circular economy and sustainable development, while also opening up new avenues for the high-value utilization of agricultural waste [45,46].

Numerous studies have confirmed that various agricultural wastes and their hydrolysates can serve as fermentation substrates for BC production. For example, a Baijiu distiller's grains and yellow water (BDY) composite medium prepared using the enzymatic hydrolysate of baijiu distiller's grains and 'yellow water' can yield BC at a rate of 7.42 g/L—3.72 times that of the HS medium—with no significant differences in product structure or performance [47]; Pineapple cores, potato juice, molasses-corn syrup mixtures, hydrolysates of pretreated rice straw, and citrus processing waste can all serve as low-cost substrates, reducing culture medium costs by more than 90% [48–54] (see Table 1).

Table 1. Strain-Specific Bioconversion of Agro-Industrial Byproducts into Functional BC with Process Control Strategies.

Microbial Strain	Agro-Industrial Waste Substrate	Process Intensification & Fermentation Strategy	Target BC Properties/Structural Features	References
<i>Komagataeibacter rhaeticus</i> QK23	artichoke bract waste	Coupling of acid hydrolysis of agricultural solids with strain-specific fermentation	Structurally functional bacterial cellulose	[55]
<i>Komagataeibacter</i> sp. HIJ12 EMCCN-4085	Bread waste hydrolysate	Box–Behnken Response Surface Method; Glycerol/Ethanol Supplementation	Large pore size three-dimensional gel structure	[56]
<i>Komagataeibacter hansenii</i> DSM 5602	Pea pod, celery root peel, and mixed-vegetable peel	Multi-source vegetable peels as a low-cost alternative carbon feedstock	Biocellulose production	[57]
<i>Novacetimonas hansenii</i> BMK-3	Papaya fruit peel waste	Direct Utilization of Papaya Peel-Based Medium and Optimization of Cultivation Conditions	Nanocellulose production	[58]
<i>Enterobacter mori</i> R45	Rice straw hydrolysates	Utilization of native strain isolated from rice plant soil	Screening of Naturally Occurring BC Strains + Optimization of Rice Straw Hydrolysate Medium	[59]
<i>Komagataeibacter xylinus</i> K2G30 (UMCC 2756)	High-stress cultivation media	Mannitol-Based Culture Medium Instead of Glucose + ALE	Increasing BC Production and Mannitol Utilization Capacity	[60]
<i>Gluconacetobacter xylinus</i>	Okara waste modified protein	Supplementation of modified protein as a nitrogen source	Fibrous bacterial cellulose with enhanced production	[61]
<i>Acetobacter xylinum</i> NBRC 13693	Various fruit juices	Fruit juice as a natural carbon source; supplementation with a nitrogen source promotes BC synthesis	Bacterial cellulose pellicle formation	[62]
<i>Komagataeibacter xylinus</i>	Wine bagasse and discarded potatoes	Co-fermentation of mixed solid agricultural residues	Active bacterial cellulose films	[63]
<i>Komagataeibacter</i> species (implied)	Grape bagasse and potato wastes	Co-production in an airlift bioreactor	Dual production of bacterial cellulose and gluconic acid	[64]

<i>Komagataeibacter xylinus</i>	Pineapple peel/core waste	Atmospheric cold plasma-assisted detoxification of hydrolysate	High-yield bacterial cellulose	[65]
<i>Komagataeibacter xylinus</i> /Microbial Consortia	Spent coffee grounds	Acid hydrolysis–enzymatic pretreatment + mannose metabolic engineering + BC membrane inoculation	Increase mannose utilization and BC yield, and improve mechanical properties	[66]
<i>Gluconacetobacter</i> species (implied)	Sugarcane straw	<i>In situ</i> fermentation of sugarcane straw with graphene	Highly conductive BC/graphene nanocomposite films	[67]
<i>Komagataeibacter rhaeticus</i>	Bread waste	Cultivation in a novel rotating disk bioreactor	Nanostructured bacterial cellulose	[68]

The chemical composition (sugar profile, proteins, organic acids, phenolic compounds, inorganic salts, *etc.*) of agricultural waste from different sources varies significantly [69]: on the one hand, it directly affects the growth, metabolism, and microbial community structure of cellulolytic strains such as *Komagataeibacter nataicola* and *Novacetimonas* sp. [69,70]; on the other hand, they can serve as metabolic precursors or regulatory signals, modulating the ultrastructure of BC—including nanofiber diameter, orientation, interlacing density, and porosity—thereby altering its crystallinity, mechanical strength, thermal stability, water retention, and adsorption properties [24,71].

Qin et al. found that non-biological factors in pre-fermented coconut water—such as lactic acid, mannitol, and ethanol—are key factors regulating the synthesis efficiency of *Komagataeibacter nataicola* [69]; adding ethanol or lactic acid to HS medium can simultaneously increase BC yield and regulate its pore structure and mechanical properties [72]. When natural fruit juices such as sugarcane juice and coconut juice are used as carbon sources, although the BC yield is slightly lower than that in HS medium, they can alter the morphology of the internal pore channels and regulate the crystallinity index [71]. Furthermore, components in waste materials—such as lignin derivatives and polyphenols—can be incorporated into the cellulose network during fermentation or serve as active sites for subsequent modification, endowing the material with intrinsic antioxidant, antibacterial, and adsorbent properties [73,74].

Elucidating the relationship between the complex components of agricultural waste and the BC biosynthetic pathway, and revealing the regulatory mechanisms by which substrates control glycolysis, UDP-glucose flux, *bcs operon* expression, and cellulase activity [41], constitutes the core scientific foundation for achieving on-demand customization of BC yield and performance [45]. Related research covers a complete technological chain encompassing waste pretreatment (physical, chemical, enzymatic hydrolysis, or microbial solid-state fermentation for sugar release and detoxification) [52,70], optimization of culture medium formulations, fermentation process control (static/dynamic/co-culture), and multiscale characterization of products [21].

3.2. Major Chemical Components of Agricultural Waste and Its Potential as a Fermentation Substrate for BC

3.2.1. Carbohydrate Components: Fermentable Sugars and Structural Polysaccharides

When used as a fermentation substrate, the carbohydrate components of agricultural waste are key factors influencing the synthesis of BC by *Komagataeibacter* spp. These components are primarily divided into two major categories: directly utilizable soluble sugars and structural polysaccharides requiring pretreatment; together, they determine the yield, structure, and even the final properties of BC.

Soluble sugars (glucose, fructose, sucrose): As the most direct carbon source for *Komagataeibacter* spp., their concentration and type have a decisive impact on bacterial growth rate and BC yield. For example, studies have shown that glucose is the optimal carbon source for *Komagataeibacter rhaeticus* to produce BC, yielding a dry BC yield as high as 7.89 g/L [75]. However, a higher concentration of the carbon source

is not necessarily better. Excessively high sugar concentrations may lead to the accumulation of metabolic byproducts (such as acetic acid and gluconic acid), thereby inhibiting bacterial growth. For instance, when using hydrolysate from pineapple peel waste (PPWH) as a carbon source, toxic compounds such as formic acid and furfural present in the hydrolysate can inhibit fermentation; detoxification treatments, such as atmospheric cold plasma (ACP), are required to increase BC yield [65]. Furthermore, different sugar sources may regulate the BC synthesis pathway by affecting the activity of key enzymes, such as cellulase. Studies have shown that *Komagataeibacter xylinum* can effectively utilize a variety of sugars; for example, it simultaneously utilizes fructose, glucose, and sucrose from loquat extract to produce BC, with utilization rates of 87.9%, 93.9%, and 100%, respectively [75]. This suggests that, in mixed sugar sources, the strain's preference for different monosaccharides and the order of their metabolism may influence the kinetics of BC synthesis.

Structural polysaccharides (cellulose, hemicellulose): Cellulose and hemicellulose in agricultural waste are abundant potential carbon sources, but they typically exist in complex lignocellulosic structures that are difficult for microorganisms to utilize directly. Therefore, efficient physical, chemical, or biological pretreatment is a necessary step to convert them into fermentable monosaccharides or oligosaccharides. The efficiency of pretreatment and the composition of hydrolysis products (such as the ratio of glucose to xylose) not only profoundly affect BC yield but may also influence the assembly process of BC nanofibers. For example, pretreating sugarcane bagasse with ionic liquids (such as methyl trioctyl ammonium chloride) is more effective than alkaline pretreatment at promoting the production of cellulase by thermophilic bacteria, thereby providing higher-quality fermentable sugars for subsequent fermentation [76]. The goal of pretreatment is to break down the stubborn structure of lignocellulose and release fermentable sugars. An efficient microbial community or synthetic microbial consortium (SynCom) can significantly enhance this process. Studies have shown that a well-designed five-member bacterial-fungal synthetic microbial consortium can increase the overall degradation rates of lignin, cellulose, and hemicellulose in co-composting of cattle manure and mulberry branches by 19.3%, 7.9%, and 12.0%, respectively [77].

The composition of the hydrolysis products is also crucial. For example, reducing sugars obtained from the hydrolysate of corn cob residue (following furfural production) were used, after detoxification, to produce BC. The productivity and yield were significantly higher than those achieved in fermentation using glucose as a substrate, while the crystallinity index of the BC increased by 43.66%, and both tensile strength and Young's modulus were significantly enhanced [78]. This suggests that the specific sugar profile derived from structural polysaccharides—which may contain pentoses or oligosaccharides other than glucose—may act as precursors or regulatory signals that influence the assembly of the cellulose synthase complex or the crystallization process of nanofibers, thereby precisely regulating the supramolecular structure and mechanical properties of BC.

3.2.2. Nitrogen Sources and Other Nutrients: Proteins, Amino Acids, and Minerals

When used as a fermentation substrate, agricultural waste contains nutrients such as proteins, amino acids, and minerals that play a crucial regulatory role in the synthesis of BC. Compared to traditional inorganic nitrogen sources (such as ammonium sulfate), the proteins in agricultural waste, after hydrolysis, provide a richer source of organic nitrogen and amino acids. These components are not only essential precursors for the synthesis of bacterial proteins and nucleic acids but also effectively promote the accumulation of bacterial biomass, thereby laying the foundation for the efficient synthesis of BC [25]. For example, protein-rich wastes such as soybean residue and brewers' grains are broken down by microorganisms during fermentation, releasing a variety of amino acids. These amino acids not only serve as nitrogen sources, but certain specific types may also act as signaling molecules or cofactor precursors, directly or indirectly regulating the activity of the cellulase complex and thereby influencing BC yield and structure [45]. Studies have shown that using agricultural waste as both a carbon and nitrogen source for

BC production is a low-cost and sustainable strategy; the complex organic nitrogen environment it provides helps maintain the stability of the fermentation system and the metabolic activity of microorganisms [25]. Furthermore, in the production of BC using the Kombucha symbiotic culture of yeast system, the addition of agricultural waste optimized nutrient supply, demonstrating the superiority of organic nitrogen sources in promoting BC biosynthesis [25].

Mineral elements in agricultural waste, such as K, Mg, Ca, Fe, and Zn, serve as inorganic nutrients required for microbial growth and metabolism, and may influence cellular physiology and product formation during the BC fermentation process. Previous studies have shown that the composition of metal ions in the culture medium can affect BC production by *Komagataeibacter*, with Mg^{2+} and Ca^{2+} believed to have a certain promoting effect on cellulose synthesis [30]. More direct biochemical studies have shown that the catalytic reaction of the bacterial cellulase *BcsA–B* depends on Mg^{2+} ; Mg^{2+} stabilizes the UDP-Glc/UDP phosphate groups and maintains catalytic activity; therefore, its availability is a critical factor for the BC polymerization reaction [79]. By regulating enzyme activity, these minerals further influence the polymerization and crystallization behavior of glucose chains during BC synthesis, ultimately exerting a significant impact on the physical properties of BC, such as crystallinity and mechanical strength [78]. A study utilizing hydrolysate from corn cob residues to produce BC found that both the yield and crystallinity index were significantly improved; this is likely due to the specific mineral components in the hydrolysate optimizing the fermentation environment [78]. Therefore, gaining a deeper understanding of the regulatory mechanisms by which mineral components in agricultural waste influence the fermentation process is a key approach to achieving precise control over the structure and properties of BC.

3.2.3. Phenolic Compounds and Inhibitory Substances: The Impact of Lignin Derivatives

When lignocellulosic agricultural waste is used as a fermentation substrate for BC, the pretreatment process is often accompanied by the degradation of lignin, resulting in the production of a series of phenolic compounds and other inhibitory substances. These substances have a dual effect on the growth and metabolism of BC-producing strains. Lignin is a complex natural aromatic polymer and one of the main components of lignocellulose; its resistance to degradation limits the effective utilization of biomass [80]. During pretreatment (such as acid, alkali, or high-temperature treatment), lignin undergoes depolymerization, yielding various phenolic monomers (such as vanillin, syringylaldehyde, p-hydroxybenzaldehyde, *etc.*), furfural, and organic acids [81]. The concentration of these substances is key to determining their functional properties. At low concentrations, certain phenolic compounds may act as inducers, stimulating bacteria to produce specific enzyme systems or altering their metabolic fluxes, which in turn may affect the activity of cellulase or the supply of precursor substances, thereby subtly regulating the degree of polymerization, crystallinity, or surface functional groups of BC [82]. For example, studies have shown that aromatic compounds produced by lignin degradation can be metabolized by certain bacteria (such as *Rhodopseudomonas palustris*) through non-classical pathways; these metabolic processes are closely related to intracellular redox balance and may indirectly influence BC biosynthesis [82]. Furthermore, phenolic compounds themselves or their oxidation products may act as precursors to cross-linking agents, interacting with the hydroxyl groups of BC and thereby altering its surface chemistry or mechanical properties [83]. However, when the concentrations of these inhibitory substances are high, they exert significant toxic effects on microorganisms. High concentrations of phenols, furfural, and other substances can disrupt cell membrane integrity, inhibit the activity of key enzymes, and interfere with cellular energy metabolism, thereby severely inhibiting the activity of production bacteria (such as *Komagataeibacter xylinum*), leading to slowed growth or even death of the bacteria, and ultimately significantly reducing BC yield [81,84]. For example, when fermenting hydrolysates derived from raw materials such as crop straw, it is essential to reduce the concentration of these inhibitory substances through detoxification treatments (such as adsorption, oxidation, or biological detoxification) to ensure the smooth

progression of the fermentation process [85]. Therefore, in processes for producing BC from agricultural waste, a thorough understanding of the formation patterns of lignin derivatives, their inhibitory mechanisms against specific production bacteria, and their concentration-dependent regulatory effects is of critical importance for optimizing pretreatment processes, developing highly efficient detoxification methods, and even utilizing their inductive effects to achieve precise control over BC performance.

3.3. Effects of Agricultural Waste Carbon Sources on Kombucha Communities and BC Synthesis

3.3.1. Effects of Carbon Source Composition on Community Structure and Function

When used as a carbon source, the hydrolysate of agricultural waste—with its complex sugar composition (such as glucose, xylose, and arabinose)—has a profound impact on the structure and function of microbial communities in kombucha fermentation systems. Compared to single carbon sources such as pure sucrose, mixed carbon sources can selectively enrich microbial strains with broader carbon utilization capabilities, thereby altering the overall diversity of the community [86]. Studies have shown that microbial communities exhibit specificity in their metabolic responses to different carbon sources, and this specificity continues to influence community composition without converging over time [87]. For example, in soil microbiology research, the addition of different carbon sources significantly alters the taxonomic composition and functional potential of bacterial communities, particularly affecting metabolic pathways related to the carbon cycle [88]. In the kombucha system, the presence of pentoses such as xylose may exert selective pressure on community structure. Studies have indicated that microbial preferences for different carbon sources are closely related to their life history strategies; for example, eutrophic bacteria (such as the *Proteobacteria* and *Bacteroidetes* phyla) tend to utilize readily available carbon sources such as glucose, whereas oligotrophic groups (such as the *Acidobacteria* phylum) have a lower ability to utilize unstable carbon sources [89]. Therefore, the mixed sugar environment provided by hydrolysates of agricultural waste may promote the growth of microbial strains capable of simultaneously metabolizing multiple monosaccharides (including pentoses and hexoses), thereby shaping a community with greater functional redundancy and metabolic flexibility [90].

The presence of specific pentoses, such as xylose, not only affects bacteria but may also significantly alter the composition of the yeast community. Certain yeasts, such as some species of the genus *Pichia*, may possess a greater metabolic capacity for pentoses [86]. This selective enrichment alters the interaction network of the entire community. For example, yeast capable of fermenting xylose may produce a different metabolite profile than that resulting from glucose fermentation (such as a different ratio of organic acids to ethanol), thereby providing differentiated substrates for other community members (such as *acetobacteria*) [86]. These changes in metabolites reshape interspecies cross-feeding networks, which in turn affect the growth and cellulase activity of bacterial cellulolytic strains (typically *Acetobacter* spp.) [86]. Analysis of physiological characteristics at the community level has also confirmed that the type of carbon source directly determines the metabolic functional characteristics of microbial communities [91]. Therefore, carbon sources from agricultural waste ultimately regulate the efficiency of bacterial cellulose synthesis by altering the relative abundance and metabolic activity of key functional strains (such as specific yeasts and *acetobacteria*).

However, growth inhibitors that may be generated during the pretreatment of agricultural waste (such as furfural, hydroxymethylfurfural, and phenolic compounds) can impose stress on the microbial community. This stress may lead to a decline in the abundance of functional strains sensitive to these inhibitors [88]. For example, under heavy metal and rare earth element stress, the structure of soil microbial communities undergoes significant changes, with an increase in the relative abundance of the *Proteobacteria* phylum, while sensitive groups such as the *Greenbacteria* and *Acidobacteria* phyla are selectively displaced [88]. Similarly, in kombucha systems, inhibitors may suppress the growth of core

cellulose-producing bacteria or key symbiotic yeasts. In response, microbial communities may evolve tolerance mechanisms. Studies have shown that under stress, microorganisms adjust their carbon source utilization strategies—for example, by prioritizing the use of phenolic and carboxylic acid carbon sources [88]—or by enhancing intraspecific cooperation to cope with environmental pressures [92]. Furthermore, the addition of exogenous carbon sources and nutrients can alter microbial community structure, inhibit harmful processes (such as acid production), and promote the abundance of beneficial functional genes [93]. Therefore, when utilizing hydrolysates from agricultural waste, optimizing pretreatment processes to remove or reduce inhibitors is crucial for maintaining the stability of the functional microbial community in kombucha and ensuring the efficient synthesis of bacterial cellulose.

3.3.2. Regulation of BC Yield and Properties

Agricultural waste, as a carbon source, has a significant impact on BC yield. The mechanism of this effect is closely related to the total amount of fermentable sugars in the waste and the efficiency with which microorganisms utilize them. Studies have shown that differences in the chemical composition and structure of various agricultural wastes result in variations in the composition and concentration of fermentable sugars in their hydrolysis products, which directly affect BC synthesis efficiency. For example, when pineapple cores from the canned pineapple industry were used as a carbon source, *Komagataeibacter xylinus* grew effectively and produced BC, with yield positively correlated with the concentration of commercial sugar in the culture medium [49]. Similarly, after detoxification treatment with atmospheric cold plasma (ACP), the BC yield from acid-hydrolyzed sugarcane bagasse reached 1.68 g/L; although this was lower than the 1.88 g/L observed in the untreated group, this suggests that the detoxification process may result in the loss of some key nutrients, thereby affecting yield [94]. Using jujube fruit waste extract as a carbon source, and by optimizing key factors such as temperature, extract percentage, and initial pH, the BC yield of the *Bacillus haynesii* strain reached as high as 2.6 g/L [95]. Together, these studies demonstrate that agricultural waste holds great potential as a carbon source, but BC yield depends directly on the availability of reducing sugars in the substrate that can be assimilated by microorganisms, as well as the presence or absence of inhibitors during fermentation. By optimizing pretreatment methods (such as ACP detoxification) and fermentation conditions, the release of fermentable sugars can be maximized, and interference from inhibitors minimized, thereby improving BC yield [65]. Furthermore, bacterial communities with lignocellulose-degrading capabilities, such as *Pseudomonas* spp. and *Actinobacteria* isolated from Keri Lake, can efficiently utilize lignocellulosic substrates. This provides a rich source of microbial resources for extracting fermentable sugars from complex agricultural waste to drive BC synthesis [96].

The type of carbon source not only affects BC yield but also profoundly determines its final physicochemical properties, including microstructure, crystallinity index, and mechanical properties. Taking xylose as an example, its use as a carbon source may lead to the synthesis of BC with different properties. Studies have confirmed that the microstructure of BC, such as fiber diameter and porosity, is influenced by the molecular structure of the carbon source and metabolic pathways. For example, through glutathione (GSH)-mediated biosynthesis, BC can be engineered to form a novel spherical branched structure, where the length and number of branches can be regulated by GSH concentration; simultaneously, the addition of GSH also results in a reduction in fiber diameter and an increase in crystallinity [97]. *In situ* addition of starch from different sources or with varying linear/branched starch content during fermentation can modulate the viscosity of the culture medium, thereby influencing bacterial motility and cellulose synthesis, and ultimately altering the porosity, pore size, and mechanical properties of the BC membrane perpendicular to the BC fiber layer [98]. BC produced from hydrolysates of agricultural waste such as corn cobs and wheat straw, exhibits characteristic bands associated with cellulose I in Fourier transform infrared spectroscopy and possesses high thermal stability; field-emission scanning electron microscopy reveals

highly ordered and densely packed fibers [24]. These variations in properties stem from differences in the assembly patterns of cellulose microfibrils during the synthesis process. Carbon sources regulate the activity of the cellulase complex and the deposition patterns of fibers by influencing bacterial metabolic flux and the intracellular levels of the second messenger c-di-GMP. For example, in *Rhizobium etli*, elevated intracellular c-di-GMP levels trigger the production of cellulose and mixed-linkage β -glucan, thereby affecting the final properties of the polymers [99]. Therefore, selecting specific agricultural waste carbon sources is one of the key strategies for the targeted production of BC materials with ideal microstructures and crystalline properties.

By optimizing the composition of agricultural waste and fermentation conditions, the physicochemical properties of BC can be specifically tailored to meet the application requirements of various fields, such as food packaging, biomedicine, and tissue engineering. Process innovations—including customized pretreatment, adaptive evolution, and specialized bioreactor design—can further enhance the scalability and product quality of BC [45]. For example, BC was produced using corn cobs and sugarcane bagasse hydrolysates under different fermentation modes—including static, continuous, and batch stirring. Results showed that stirring conditions (particularly continuous stirring) yielded higher BC yields, and the resulting BC exhibited excellent mechanical properties; for instance, BC produced by a certain strain under batch stirring conditions using corn cobs achieved an elastic modulus of up to 10.8 GPa and a tensile strength of 70.9 MPa [24]. Adaptive laboratory evolution (ALE) is an effective strategy; through long-term continuous cultivation of *Komagataeibacter xylinus* K2G30 in mannitol medium, the strain was phenotypically improved, resulting in a 38% increase in BC yield. Furthermore, this adaptation did not come at the expense of glucose utilization, demonstrating the strain's metabolic versatility in producing BC from different carbon sources [60]. Furthermore, engineering production strains through genetic engineering and synthetic biology allows for more precise regulation of BC synthesis. For example, overexpression of the luxR gene in the quorum sensing system increased BC yield in *Gluconacetobacter xylinus* CGMCC 2955 by 15.6% and altered the composition of the signaling molecule AHL, thereby influencing metabolic pathways [100]. *In situ* modification during fermentation—such as introducing the hyaluronan synthase and UDP-glucose dehydrogenase genes into *Gluconacetobacter hansenii*—enables the simultaneous production of hyaluronan and BC, resulting in gel-like nanocomposites with superior performance [101]. These regulatory approaches enable the customized production of BC, such as for the fabrication of gradient-porous Janus films with enhanced optical properties and thermal-humidity comfort for radiative cooling [102], or for the preparation of programmable BC microfibers with high tensile strength (~115 MPa) suitable for surgical sutures [103]. Therefore, the systematic integration of carbon source selection, process optimization, and strain engineering is the only way to develop high-performance BC materials that meet the specific requirements of particular applications.

3.4. Techno-Economic Analysis and Environmental Sustainability

The imperative primarily drives the transition toward industrial crop byproducts to harmonize economic profitability with environmental stewardship. Techno-Economic Analysis (TEA) and Life Cycle Assessment (LCA) provide the quantitative foundation for this feasibility.

3.4.1. Economic Feasibility and Commercial Viability

Raw material costs, energy intensity, and equipment depreciation dominate the economic profile of BC production. Conventional media rely on expensive, refined components such as glucose and peptone. Recent studies have demonstrated that recycling tea waste or utilizing black molasses can reduce media [104].

Remarkably, Ciecholewska et al. (2024) reported that utilizing potato juice media could slash the cost of producing 1 kg of BC from over €1200 (HS medium) to approximately €60—a staggering 95% reduction

[50]. From a capital investment perspective, a TEA of a 60-ton-per-year facility revealed a promising Return on Investment (ROI) of 23.64% and a payback period of 4.23 years [105]. As feedstock costs shift from high-value inputs to “negative cost” waste streams (where processors pay for disposal), the Net Present Value (NPV) and commercial attractiveness of BC production improve exponentially.

The overall cost of BC production is primarily determined by the cost of raw materials—particularly carbon sources—along with energy consumption and equipment depreciation. Conventional HS medium contains expensive ingredients, such as glucose, peptone, and yeast extract. Avcioglu et al. (2021) established a composite microbial consortium for kombucha and partially replaced the nitrogen source with black tea. Under optimized conditions, it achieved a BC of 18.68 g/L—a 4.06-fold increase compared to HS medium—while reducing cultivation costs by 29.74%. This strategy enabled high-yield, low-cost production of BC [106]. Selvaraj et al. (2024) used the Taguchi-response surface method to optimize the SCOBY cultivation system, using tea powder and molasses as low-cost nutrient sources. This reduced the cost of the culture medium from \$0.075 to \$0.027 per liter, while increasing the SCOBY yield to 2.56% [104]. Similarly, Pandey et al. (2024) estimated that substituting glucose with molasses cuts production costs from \$175/kg to \$85.08/kg, representing a more than 50% reduction [107].

3.4.2. Environmental Viability and the Circular Bioeconomy

Beyond cost-efficiency, the utilization of agro-industrial byproducts offers transformative environmental benefits: (1) Waste Valorization: Transforming voluminous waste streams into high-value biopolymers mitigates the ecological burden of landfilling and incineration [19]. (2) Carbon Footprint Mitigation: By bypassing the energy-intensive refining processes required for commercial sugars, waste-derived BC significantly lowers the cumulative energy demand. LCA studies confirm a substantial reduction in Global Warming Potential (GWP) when using brewing or agricultural residues [108]. (3) Circular Economy Integration: This approach establishes a closed-loop biorefinery model, where “waste” from the food and agricultural sectors becomes the “feedstock” for advanced materials manufacturing, fostering cross-sectoral sustainability [109].

Although agricultural waste can significantly reduce raw material costs, processes such as waste collection, transportation, pretreatment, sterilization, and downstream separation and purification of bacterial cellulose still drive up the overall production costs [45]. Lignocellulosic feedstocks are subjected to physical, chemical, or biological pretreatment to release fermentable sugars; this process is generally characterized by high energy consumption, long cycle times, and the risk of secondary pollution. At the same time, the sterilization of large-scale fermenters also results in high energy consumption.

During process scale-up, shallow-bed static fermentation exhibits significant engineering limitations. Due to mass transfer constraints, the uneven distribution of nutrients and oxygen within the reactor inhibits the proliferation of the SCOBY microbial community and reduces the efficiency of bacterial cellulose synthesis; heat accumulation in the reactor further causes temperature inhomogeneity, disrupting the stability of the fermentation system.

To improve process economics, future research should focus on developing highly efficient, low-energy-consumption integrated technological pathways. On the one hand, static cultivation systems that do not require strict sterilization (such as the kombucha symbiotic fermentation system) can be developed, and highly stress-tolerant engineered strains capable of directly utilizing complex substrates can be selected and bred [25]; on the other hand, the structural design of equipment such as upflow reactors could be optimized to enhance mass transfer efficiency and thereby increase production capacity. Integrating bacterial cellulose production into the circular bioeconomy framework to achieve the resource utilization of all waste components is also a key strategy for reducing overall costs and promoting large-scale application [45,110].

In conclusion, while initial investments in pretreatment infrastructure are required, the integration of byproduct-based feedstocks offers unparalleled long-term operational advantages, positioning BC as a cornerstone of the sustainable bio-based industry.

4. Advanced Strategies: High-Yield Strains and Genetic Engineering

The SCOBY constitutes a sophisticated fermentation consortium, where coordinated metabolic syntrophy drives the biosynthesis of BC. The primary functional pillars of this consortium include AAB, yeasts, and lactic acid bacteria (LAB) [111]. Despite its immense biotechnological potential, the industrial scaling of BC is currently bottlenecked by low space-time yields, suboptimal strain stability, and prohibitive substrate costs [112]. Recent research has pivoted toward the isolation of high-performance wild-type strains, the rational design of microbial consortia [113], and the precision engineering of microbial cell factories to enhance the economic viability of kombucha-derived BC.

4.1. Screening and Characterization of High-Efficiency Strains

The yield and structural attributes of BC are intrinsically dictated by the specific microbial architecture of the SCOBY. Within the *Komagataeibacter* genus, BC productivity is highly strain-dependent (see Table 2). While *Komagataeibacter xylinus* remains the gold standard for BC production, substantial phenotypic variability exists even among closely related isolates, making rigorous strain selection a prerequisite for industrialization [20].

Modern strain identification leverages a polyphasic approach, combining morphological and biochemical profiling with 16S rRNA gene sequencing and comparative genomics [114]. For instance, Landis et al. (2022) revealed that despite >99% genomic similarity, *Komagataeibacter* species can exhibit fivefold differences in BC output [115]. To enhance screening throughput, molecular fingerprinting—such as (GTG)_n repetitive sequence analysis and ERIC-PCR—has achieved a discrimination index (D-index) of 0.94, significantly streamlining the identification of elite producers [20].

Application-oriented studies have underscored the potential of “niche-specific” strains. For example, *K. rhaeticus* QK23, isolated from kombucha, demonstrated robust performance on asparagus waste [116], while *K. xylinus* exhibits high cellulose synthase (Cela) activity and superior adaptability to complex carbon sources [117].

4.2. Optimization and Rational Design of the Symbiotic Consortium

The SCOBY represents a rapidly renewable “natural bioreactor”. Its community is typically dominated by *Komagataeibacter* (36.24–63.35%), with significant contributions from *Gluconobacter* and the fungus *Kluyveromyces* [118].

Optimization of this symbiotic system follows three primary trajectories:

- (1) Mutagenesis and ALE: Ultraviolet (UV) irradiation and ethyl methyl sulfonate (EMS) mutagenesis can be used to obtain and screen high-yield mutant strains of BC. Furthermore, serial subculturing of ALE of *K. xylinus* K2G30 over 30 generations resulted in a 38% increase in yield by enhancing mannitol utilization [60].
- (2) Synthetic Co-culture Engineering: Co-fermentation of *K. xylinus* with yeasts like *Saccharomyces bayanus* has achieved yields of 12.13 g/L in coconut water media, while concurrently enhancing the mechanical and antibacterial properties of the BC membrane [119].
- (3) Metabolic Tailoring: This study proposes a three-pronged recommendation for optimizing SCOBY consortia: (i) Select a *Komagataeibacter* strain with high biosynthetic flux; (ii) Pair with acid-tolerant, ethanol-productive yeasts; and (iii) Integrate acid-tolerant LAB to establish a rapid protective pH barrier and amplify BC synthesis via metabolic signaling.

4.3. Synthetic Biology and Gene Editing in BC Production

Genetic engineering offers a transformative pathway for bypassing the natural limits of BC biosynthesis. Synthetic biology tools, particularly CRISPR-based systems, enable the rational rewiring of metabolic pathways to maximize carbon flux toward cellulose [120].

Key genetic interventions include:

- (1) Targeting the *bcs Operon*: Overexpression of *bcsC* and *bcsD* genes facilitates more efficient cellulose chain secretion and crystallization, improving both yield and thermal stability [121]. Regulating the expression of the *bcsABCD* genes significantly enhances BC synthesis. By using an arabinose-inducible promoter to regulate the *bcsABCD operon*, the BC yield in *K. xylinus* was increased approximately fourfold, and a thicker BC film was formed [122].
- (2) Expanding Substrate Breadth: Metabolic reconstruction of the mannose catabolic pathway in *K. xylinus* ATCC 23770 enabled efficient mannose utilization, yielding an 84% increase in BC production and significant improvements in Young's modulus [123].
- (3) Enhancing carbon metabolism regulation: The *pfkA* gene was introduced, and the global carbon metabolism regulator *crp* was expressed to construct the *S. Koma-pfkA/crp* strain, thereby restoring the glycolytic pathway and redistributing central carbon metabolism fluxes. Following optimization of the fermentation process, the glucose conversion yield of BCNF increased from 9.5% to 31.5%, while the yield of the byproduct gluconic acid decreased from 64.8% to 39.2%, and fermentation production on a 30-L scale was successfully achieved [124].

Critical Challenges in Genetic Engineering:

Despite these advances, the application of engineered strains in SCOPY systems faces several hurdles:

- (1) Genetic Tooling Gaps: Genetic transformation and genetic engineering of *Komagataeibacter* are still limited by the availability of genetic tools and differences in the genetic backgrounds of strains, which in turn hinder the establishment of an efficient genetic modification system [125].
- (2) Ecological Disequilibrium: Introducing engineered strains may disrupt the delicate competitive/cooperative balance of the indigenous consortium, potentially compromising stability.
- (3) Inhibitor Sensitivity: Lignocellulosic hydrolysates often contain furfural or phenolic inhibitors; thus, developing multi-stress-tolerant strains through targeted gene editing remains a high priority for industrial “waste-to-wealth” applications.

Table 2. Strategies and Performance Optimization for Gene Modification to Enhance BC yield.

Gene Modification Strategies	Target Strain	Key Genes/Pathways	Yield Increase	Improvement of Material Properties	References
Carbon-source adaptation/metabolic engineering	<i>K. Xylinus</i> K1G4	Mannitol Metabolic Pathway	Improved BC yield	Improved utilization of alternative carbon sources	[20]
Overexpression of cellulose synthase genes	<i>Gluconacetobacter xylinus</i>	<i>bcsC</i> , <i>bcsD</i>	2.2 → 5.4–6.8 g/L	↑ tensile strength, crystallinity, degree of polymerization and thermal stability, particularly with <i>bcsD</i>	[121]
Mannose metabolic pathway engineering	<i>K. Xylinus</i> ATCC 23770	<i>mak</i> , <i>pmi</i>	+84% on mannose medium	Tensile strength 1.7-fold; Young's modulus 1.3-fold	[123]
Metabolic engineering of glycolytic flux	<i>Komagataeibacter</i> sp. <i>S. Koma</i> -pfkA/crp	<i>pfkA</i> , <i>crp</i>	BCNF yield increased from 9.5% to 31.5% (~3.3-fold)	High-productivity BCNF; demonstrated in 30-L fermentation	[124]

Synthetic RBS-mediated pathway engineering	<i>Komagataeibacter xylinus</i>	<i>pgm, galU, ndp</i>	BC titer reached 5.28 g/L under static culture and 3.67 g/L under shaking culture	Enhanced metabolic flux toward BC biosynthesis [126]
High hydrostatic pressure-induced mutagenesis	<i>Gluconoacetobacter xylinus</i> J2	Random mutagenesis and screening	BC yield improved significantly, with the optimal mutant achieving 158.56 g/L	Obtained genetically stable high-yield mutant with a variation coefficient of only 2.4% [127]
UV mutagenesis + ALE related strain	<i>K. sucrofermentans</i> -PP177480	Genome-wide adaptive evolution	>6-fold, 9.3 g/L vs. 1.31 g/L	Larger nanopores; cellulose I; crystallite size increased [128]

5. Circular BC Production: Integrating Biorefinery for Total Waste Valorization

The key to shifting BC production toward a circular production model lies not simply in increasing bacterial cellulose yield, but in achieving the cascading utilization of carbon sources, nutrients, and fermentation byproducts in the raw materials. In systems using agricultural and food byproducts as culture media, fermentable components are first converted by microorganisms into bacterial cellulose; meanwhile, underutilized sugars, organic acids, and other soluble organic compounds remain in the fermentation waste liquid. Therefore, fermentation waste liquid should not be viewed merely as end-of-pipe wastewater; it can be further valorized through methods such as recirculating inoculation, component recovery, and anaerobic digestion to achieve the reuse of materials and energy, thereby reducing waste discharge and improving the overall resource utilization efficiency per unit of raw material [129–131]. This “feedstock—fermentation—product—byproduct—reuse” cascading model lays the foundation for the transition of bacterial cellulose production from a single biomanufacturing process to a circular biorefining system.

5.1. Recycling and Resource Recovery of Used Kombucha Culture Medium

The Spent Culture Medium (SCM), traditionally discarded as a high-COD (Chemical Oxygen Demand) pollutant, is a reservoir of valuable co-products, including organic acids (acetic, gluconic, and glucuronic acids), residual sugars, ethanol, and bioactive metabolites [132].

5.1.1. Closed-Loop Inoculum and Antimicrobial Barrier

Implementing a recirculating back-slopping system, stabilizes the microbial succession and reduces overall fermentation times [133]. Metagenomic sequencing of continuous back-slopping fermentations indicates that the low pH (2.8 ± 0.3) of the SCM selectively inhibits competing pathogenic or wild microorganisms, thereby maintaining a stable core microbiota dominated by the *Komagataeibacter* and *Zygosaccharomyces* genera across multiple generations [134,135]. This ecological stability ensures reproducible BC yields and preserves the bacterial nanocellulose nanofibrillar structure, avoiding the phenotypic drift and yield decline commonly observed during the long-term propagation of pure monocultures [136]. Furthermore, the antimicrobial organic acids can be recovered for industrial textile pretreatments or used to suppress enteric pathogens like *E. coli* and *Salmonella*, showcasing immense potential in medical and sanitary applications [137]. Glucuronic acid (GlcUA), another important metabolite generated during kombucha fermentation, is involved in glucuronidation and has been proposed to contribute to the antioxidant and hepatoprotective potential of kombucha, further supporting the value of SCM as a potential source of bioactive compounds [113].

5.1.2. Energy Recovery via Anaerobic Digestion

Research shows that by utilizing 5800 metric tons of glycerol by-products generated annually by Brazil's biodiesel industry, it is possible to achieve a monthly production capacity of 63 metric tons of BC. By treating the wastewater generated from BC production at this scale using an anaerobic sequenced batch reactor (ASBR) with a volume of $2.8 \times 10^4 \text{ m}^3$, methane produced through biogas fermentation can generate $3.2 \times 10^2 \text{ kW}$ of electricity. This system can simultaneously achieve wastewater purification and clean energy production, helping the BC production process meet the dual goals of harmless wastewater treatment and energy self-sufficiency [23].

5.1.3. Emerging Frontier: Bioleaching of Strategic Metals

A transformative application of SCM is its use as a "green" leaching agent for heavy metal recovery. The protons (H^+) and organic acid anions in the broth can effectively destabilize metal oxide lattices in spent lithium batteries or manganese ores. Recent studies achieved a 26.3% extraction rate for manganese using kombucha SCM under mild conditions [138]. This "waste-to-waste" treatment model offers a sustainable alternative to corrosive inorganic acids.

5.2. Functional Applications of Byproduct-Derived BC Materials

BC synthesized from industrial residues often inherits unique functionalities or enhanced performance tailored for diverse sectors:

- (1) **Biomedical Scaffolds:** The nanoporous architecture of waste-derived BC makes it a premier candidate for wound dressings. Integrating pomegranate peel extracts or silk sericin into the BC matrix confers superior antimicrobial and UV-shielding properties [139,140].
- (2) **Flexible Electronics and Energy Storage:** Byproduct-derived BC serves as a sustainable precursor for nitrogen-doped porous carbon electrodes. These materials are used in high-performance supercapacitors, lithium battery separators, and wearable strain sensors [141,142].
- (3) **Environmental Remediation:** BC-based adsorbents effectively sequester dyes and heavy metals from wastewater. Engineered "Syn-SCOBY" systems have further extended this utility to the enzymatic degradation of β -lactam antibiotics and endocrine disruptors [143].
- (4) **Sustainable Leather Alternatives:** BC membranes grown from tea residues or whey exhibit exceptional tensile strength and modulus, rivaling traditional leather. This positions kombucha-BC as a cornerstone of the vegan leather industry and advanced tissue engineering [117,144].

6. Conclusions and Perspectives

This review highlights kombucha SCOBY as a promising biomanufacturing platform for converting agricultural byproducts into bacterial cellulose. By establishing the Feedstock–Strain–Property–Application framework, this work connects feedstock composition with microbial interactions, cellulose biosynthesis, and the resulting structural and functional properties of BC, providing a more systematic perspective than conventional substrate-based evaluations.

Agricultural byproducts can supply diverse carbon and nutrient sources, while their endogenous phenolics, organic acids, and other components may further influence microbial metabolism and BC formation. Accordingly, feedstock selection should be considered not only as a strategy for reducing medium costs, but also as an approach for regulating BC structure and properties. At the same time, feedstock variability, inhibitory compounds, pretreatment, mass transfer, and downstream processing remain important barriers to process stability and scale-up.

The integration of microbial community optimization, process intensification, and full-chain resource utilization will therefore be essential for translating this platform into practical biomanufacturing. Future

studies should further clarify the feedstock–microbiome–material relationships through multi-omics and data-driven approaches, while validating economic and environmental performance at the pilot scale.

Overall, the SCOPY-based FSPA framework provides a useful basis for advancing agricultural byproduct valorization, moving from low-cost substrate substitution to the rational production of high-value, application-oriented BC materials.

Statement of the Use of Generative AI and AI-Assisted Technologies in the Writing Process

During the preparation of this manuscript, the authors used ChatGPT and DALL-E 3 (OpenAI) to improve English language readability and to generate the schematic illustrations in this review. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the article.

Author Contributions

Y.H.: Conceptualization, Writing—original draft, Formal analysis, Validation, Visualization, Writing—review & editing. H.Z. and C.G.: Methodology, Investigation. M.L.: Validation, Investigation. K.C.: Software, Visualization. Z.L.: Validation, Methodology, Supervision. S.C.: Conceptualization, Validation, Resources, Writing—review & editing, Supervision, Project administration, Funding acquisition. All authors agreed with the publication of the manuscript.

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Declaration of Competing Interest

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

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