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BACTERIAL CELLULOSE: ADVANCES AND CHALLENGES

Bacterial cellulose (BC) is a highly pure, crystalline biopolymer synthesized by a variety of microbial species, offering remarkable mechanical strength, high water-holding capacity, and excellent biocompatibility. These unique physicochemical properties have driven extensive research into BC-based materials for biomedical devices, wound dressings, tissue engineering scaffolds, controlled drug delivery systems, sustainable packaging, filtration membranes, and flexible or wearable electronics. Unlike plant-derived cellulose, BC is free from lignin, hemicellulose, and other biomass-associated impurities, resulting in a nanofibrillar network with high crystallinity and tunable porosity. However, despite its advantages, large-scale industrial utilization remains constrained by high production costs, slow fermentation rates, and challenges related to process scale-up and strain stability. Recent strategies to overcome these limitations include the optimization of culture media using agro-industrial residues, bioreactor engineering to enhance oxygen transfer and productivity, co-culture systems to boost metabolic efficiency, and genetic or synthetic biology approaches to reprogram biosynthetic pathways. Additionally, emerging applications such as BC-based composite materials, bioinks for 3D bioprinting, and functionalized scaffolds for regenerative medicine highlight the growing translational potential of BC research. This review provides an integrated overview of BC-producing microorganisms, technological bottlenecks, economic considerations, and current advances aimed at improving scalability, sustainability, and commercial viability. Finally, key outlooks for future innovations and industrial deployment are discussed.

Keywords: bacterial cellulose, biomass, biopolymer, sustainable packaging, agro-industrial by-products, scale-up.

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Бактериялық целлюлоза: жетістіктері мен қиындықтары

Бактериялық целлюлоза (БЦ) – әртүрлі микробтық түрлер арқылы синтезделетін жоғары тазалықтағы, кристалды құрылымды биополимер, ол ерекше механикалық беріктігімен, суды жоғары мөлшерде ұстау қабілетімен және тамаша биосәйкестік қасиеттерімен ерекшеленеді. Осындай бірегей физика-химиялық сипаттамалары БЦ негізіндегі материалдарды биомедициналық құрылғыларда, жара таңғыштарында, тіндік инженерияға арналған тірек құрылымдарында, бақыланатын дәрі жеткізу жүйелерінде, экологиялық тұрғыдан тұрақты орау материалдарында, сүзгілеу мембраналарында, сондай-ақ икемді және киілетін электроникада қолдануға кең мүмкіндік ашады. Өсімдік текті целлюлозадан айырмашылығы, БЦ құрамында лигнин, гемицеллюлоза және басқа да қоспалар болмайды, нәтижесінде жоғары кристалдылыққа ие наноталшықты құрылым түзіледі және оның кеуектілігі мен морфологиясын басқаруға болады. Дегенмен осы артықшылықтарына қарамастан, БЦ өндірудің кең ауқымды өнеркәсіптік қолданылуы жоғары өндірістік шығындармен, ферментацияның баяу жүруімен, штаммдардың тұрақтылығын қамтамасыз ету және процесті масштабтау қиындықтарымен шектеледі. Осы

бағытталған соңғы әдістемелерге агроөнеркәсіптік қалдықтарды қолдану арқылы қоректік орталарды оңтайландыру, оттегіні жеткізу мен өнімділікті арттыруға арналған биореактор инженериясы, метаболикалық үйлесімділікті күшейтетін ко-мәдениет жүйелері, сондай-ақ биосинтетикалық жолдарды қайта бағдарлауға мүмкіндік беретін генетикалық және синтетикалық биология тәсілдері жатады. Сонымен бірге БЦ негізіндегі композиттік материалдар, 3D биобаспаға арналған биоинктер және регенеративті медицинаға арналған функционалдандырылған матрицалар саласындағы жаңа бағыттар БЦ зерттеулерінің трансляциялық әлеуетінің артып келе жатқанын көрсетеді. Бұл шолуда БЦ өндіретін микроорганизмдер, технологиялық және экономикалық шектеулер, сондай-ақ масштабтау, тұрақтылық және коммерцияландыруды жақсартуға бағытталған қазіргі ғылыми жетістіктер жан-жақты қарастырылады.

Түйін сөздер: бактериялық целлюлоза, биомасса, биополимер, экологиялық орау, агроөнеркәсіптік жанама өнімдер, масштабтау.

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Бактериальная целлюлоза: достижения и проблемы

Бактериальная целлюлоза (БЦ) представляет собой высокочистый, кристаллический биополимер, синтезируемый различными микроорганизмами и обладающий выдающейся механической прочностью, высокой влагоудерживающей способностью и превосходной биосовместимостью. Благодаря таким уникальным физико-химическим свойствам материалы на основе БЦ находят широкое применение в биомедицинских устройствах, раневых покрытиях, каркасах для тканевой инженерии, системах контролируемой доставки лекарств, экологически устойчивых упаковочных материалах, фильтрационных мембранах, а также в гибкой и носимой электронике. В отличие от растительной целлюлозы, БЦ не содержит лигнин, гемицеллюлозу и другие сопутствующие примеси, что обеспечивает формирование нанопибриллярной структуры с высокой степенью кристалличности и возможностью регулирования её пористости и морфологии. Несмотря на значительные преимущества, широкомасштабное промышленное производство БЦ ограничено высокими затратами на культивирование, медленной кинетикой ферментации, необходимостью поддержания стабильности продуцирующих штаммов и трудностями масштабирования технологических процессов. Для преодоления этих ограничений в последнее время активно развиваются подходы по оптимизации питательных сред с использованием агропромышленных побочных продуктов, инженерия биореакторов для улучшения передачи кислорода и повышения производительности, системы совместных культур для усиления метаболических потоков, а также методы генетической и синтетической биологии для перенастройки биосинтетических путей. Кроме того, перспективные направления включают создание композитных материалов на основе БЦ, разработку биочернил для 3D-биопечати и функционализированных матриц для регенеративной медицины. Данный обзор обобщает современные знания о микроорганизмах-продуцентах БЦ, технологических и экономических барьерах её производства, а также последних достижениях, направленных на повышение масштабируемости, устойчивости и коммерциализации данного биополимера.

Ключевые слова: бактериальная целлюлоза, биомасса, биополимер, экологичная упаковка, агропромышленные побочные продукты, масштабирование.

Abbreviations: BC – bacterial cellulose, EPS – exopolysaccharides, HS – Hestrin–Schramm medium, LCA – life cycle assessment

1. Introduction

Cellulose is the most abundant natural polymer on Earth, traditionally sourced from plant biomass [1]. However, bacterial cellulose (BC), first ob-

served by Adrian J. Brown in 1886, has emerged as a superior alternative due to its remarkable purity, unique nanofibrillar architecture, and exceptional physicochemical properties [2-4]. Unlike plant-derived cellulose, BC is synthesized free of lignin, hemicellulose, and other contaminants, resulting in a highly crystalline, ultra-fine fibril network with a degree of polymerization exceeding 10,000 units and crystallinity indices above 80% [5, 6]. These

structural advantages translate into a tensile strength typically ranging from 0.2 to 1.2 GPa and a Young's modulus of 15–35 GPa, while its water-holding capacity can exceed 1,000% of its dry weight, markedly outperforming conventional cellulose materials [7, 8].

Over the past two decades, research on BC has intensified, driven by its broad application potential [7]. In biomedical engineering, BC's biocompatibility and porous architecture have been harnessed for wound dressings that accelerate tissue regeneration and for vascular grafts capable of supporting endothelialization [8]. For instance, Czaja et al. (2007) demonstrated that BC membranes impregnated with silver nanoparticles exhibit potent antimicrobial activity [9], while Janmohammadi et al. (2022) reported BC-based scaffolds promoting osteoblast proliferation for bone tissue engineering [10]. In the realm of drug delivery, *in situ* functionalization of BC with pH-responsive polymers has enabled controlled release systems for chemotherapeutics, achieving sustained drug liberation over multiple days [11].

Beyond healthcare, the intrinsic flexibility and mechanical robustness of BC have spurred its integration into flexible electronics and sensors. Rashid et al. (2024) developed a BC–graphene composite as a highly sensitive strain sensor with a gauge factor above 200 [12], while Luo et al. (2019) fabricated a BC-based substrate for transparent, bendable electrodes in organic light-emitting diodes [13]. Filtration technologies have also benefited: Qi et al. (2017) engineered nanoporous BC membranes capable of sieving viruses and heavy-metal ions with over 99% removal efficiency under low pressure [14]. Sustainable packaging is another burgeoning field, where BC films reinforced with chitosan provide compostable, gas-barrier materials suitable for food preservation.

Despite these successes, commercialization of BC remains constrained by high upstream costs and scale-up complexities. Conventional Hestrin-Schramm (HS) medium, composed of glucose, yeast extract, and peptone, can account for over 60% of production expenses, while static culture methods yield only 1–2 g/L over 7–10 days [15]. To address this, recent studies have explored the valorization of agro-industrial residues. For example, Wu and Liu (2012) achieved BC titers of 10 g/L using thin stillage from ethanol distilleries [16], and Güzel et al. (2018) obtained 5.5 g/L on citrus peel hydrolysate with minimal pretreatment [17]. These approaches not only reduce raw-material costs by up to 70% but

also align BC production with circular bioeconomy principles.

Genetic and metabolic engineering strategies have further expanded BC productivity and functionality. Hur et al. (2018) used CRISPR interference to repress glucose dehydrogenase in *Komagataeibacter xylinus*, diverting carbon flux toward cellulose synthesis and increasing yields by 2.3-fold [18]. Advances in bioreactor design, such as airlift, rotating disk, and perfusion systems, have demonstrated volumetric productivities exceeding 5 g/L/day while maintaining fibril integrity [19]. Online process analytics for dissolved oxygen, pH, and redox potential have been employed to safeguard consistent quality across scales.

This review provides a system-level synthesis of the major BC producers and their metabolic traits, technical and economic bottlenecks and mitigation strategies, as well as future directions including biorefinery integration, BC-based bioinks, and life-cycle assessments. In contrast to previous reviews that typically focus on either material properties or production optimization in isolation, this work integrates microbial diversity, metabolic and genetic engineering approaches, co-culture strategies, the use of low-cost substrates, and scale-up considerations to support the advancement of BC production toward industrial implementation.

2. Optimization of BC production

Optimization of BC production involves improving strain performance, regulating metabolic pathways, and adjusting cultivation conditions to increase yield and material quality. Key strategies include selection or engineering of high-producing strains, co-culture approaches to enhance precursor supply, and process scale-up using low-cost substrates and controlled bioreactor environments (Figure 1).

2.1. Identification of potential cellulose-producing bacteria

A diverse array of bacterial genera have been identified and exploited for their BC-synthesizing capabilities, each offering unique advantages in terms of yield, fibril structure, and ease of cultivation [20].

Numerous studies have documented a remarkably diverse spectrum of bacterial (and even some protist) genera capable of synthesizing BC under a variety of conditions. Notably, *Komagataeibacter* sp., *Agrobacterium* sp. and *Enterobacter* sp. have all

been shown to produce substantial BC yields when grown on defined media [21]. In addition to these, several soil- and plant-associated microbes, such as *Rhizobium* sp. and *Lactobacillus* sp., have emerged as promising BC producers thanks to their ability to utilize complex carbon sources, as reported by Li et al. (2021) [22].

Going further back, early work by Carreira et al. (2011) identified *Sarcina* sp. as a source of amorphous cellulose with unique gel-forming properties [23], while Ye et al. (2019) demonstrated that *Acetobacter* sp. can generate highly crystalline BC suitable for electronic and biomedical applications [24]. More recently, Ghazali et al. (2021) expanded the roster of BC-synthesizers to include both *Azotobacter* sp. and the versatile *Pseudomonas* sp., underscoring the breadth of metabolic strategies bacteria employ to assemble nanofibrillar cellulose [25].

Beyond these well-studied groups, less conventional taxa have also been reported, including *Alcaligenes* sp. [27, 28] and additional *Gluconacetobacter* strains, which have been optimized for higher BC titers through medium engineering [29]. In contrast, *Leifsonia soli*, a soil-dwelling actinobacterium, has been reported to synthesize BC with unusually long fibrils, highlighting broader phylogenetic diversity among non-acetic acid BC producers [30, 31]. Moreover, photosynthetic Cyanobacteria and *Rhodococcus* sp. [26] have been shown to contribute to BC pools in mixed cultures, while Yim et al. (2017) described a marine-derived *Rhodobacter* sp. strain that forms robust pellicles under saline conditions [27]. Common to all these organisms is the ecological imperative to produce cellulose: it facilitates oxygen diffusion to cells for aerobic metabolism, offers protection against harmful ultraviolet radiation, and serves as a hydration reservoir in otherwise desiccating environments [28].

Komagataeibacter xylinus (formerly *Gluconacetobacter xylinus*) remains the model organism for BC production, owing to its high cellulose output and well-characterized operon [29]. In static culture, *K. xylinus* forms gelatinous pellicles at the air-liquid interface, while agitated cultures can yield irregular aggregates unless process parameters (e.g., shear stress, dissolved oxygen) are optimized [30]. Genetic tools have been developed to modulate expression of cellulose synthase genes, enabling the tuning of fibril diameter and crystallinity [31].

Other *Komagataeibacter* species, such as *K. hansenii* and *K. rhaeticus*, have demonstrated robust growth on agro-industrial residues, including fruit pomaces and crude glycerol, with BC yields comparable to those in HS medium [25, 32]. In particular, *K. hansenii* strains have been shown to produce uniform films on coffee cherry husk hydrolysate, highlighting the potential for valorizing waste streams [33].

Beyond acetic acid bacteria, genera such as *Rhizobium*, *Azotobacter*, and *Sarcina* have been explored for BC synthesis. *Rhizobium* sp. can generate both crystalline and amorphous cellulose matrices suitable for composite materials, while *Azotobacter vinelandii* can co-produce alginate and cellulose, offering dual biopolymer systems for advanced applications [6]. *Sarcina* spp. produce amorphous cellulose that has been investigated for biosensor backbones and immobilization matrices [34].

Recently, efforts to engineer *Escherichia coli* with BC synthase operons have enabled rapid genetic prototyping and the incorporation of non-native modifications, such as *in situ* functionalization with peptides or polysaccharides [35]. Although yields in recombinant hosts remain lower than native producers, synthetic biology approaches promise fine control over BC architecture and composition (Table 1).

Table 1 – Main bacteria actively used in BC production: substrates and culture conditions

Microorganism	Low-Cost Substrate	Cultivation Conditions	BC (g/L)	References
<i>Komagataeibacter xylinus</i>	Corn steep liquor is a byproduct of the maize wet-milling industry; it contains abundant amino acids, vitamins and minerals that support high-density bacterial growth and robust cellulose pellicle formation.	30 °C	12	[36]
<i>Komagataeibacter sucrofermentans</i> DSM15973	20 g/L pGLYC or 20 g/L cGLYC, 5 g/L YE, 5 g/L Pep, 1.1 g/L citric acid	30 °C	1.9	[37]

Continuation of the table

Microorganism	Low-Cost Substrate	Cultivation Conditions	BC (g/L)	References
<i>Gluconacetobacter xylinus</i>	Thin stillage is the liquid fraction remaining after ethanol distillation; it is rich in residual sugars, amino acids, and yeast nutrients, making it an economical feedstock for static pellicle production.	30 °C, static, 7 d	10	[16]
<i>Gluconacetobacter sacchari</i>	Dry olive mill residue comprises the solid waste from olive oil extraction, containing residual lipids, phenolic compounds and carbohydrates; after simple drying it can be used as a carbon and energy source for BC synthesis.	30 °C, static, 96 h	0.8	[38]
<i>Komagataeibacter rhaeticus</i> ENS9a	Pure glycerol (20 g/L); Crude glycerol (20 g/L)	30 °C, static, 96 h	2.6	[39]
<i>Gluconacetobacter hansenii</i>	Waste brewery yeast consists of spent yeast biomass from beer production; after mild acid or enzymatic hydrolysis it releases peptides, B-vitamins and polysaccharides that support high cellulose yields over a 14-day static culture.	30 °C, static, 14 d	7.0	[40]
<i>Gluconacetobacter xylinus</i>	Thin stillage wastewater from distilleries contains fermentable sugars and volatile organic acids; recycling this effluent reduces discharge costs while providing essential nutrients for a 7-day static pellicle.	30 °C, static, 7 d	6.6	[16]
<i>Gluconacetobacter xylinus</i>	Carob and haricot bean residues are agro-industrial legume wastes rich in complex carbohydrates and proteins; enzymatic or acid pretreatment breaks them down into fermentable sugars for static 9-day cellulose synthesis.	30 °C, static, 9 d	3.3	[41]
<i>Gluconacetobacter xylinus</i>	Lipid fermentation wastewater is an oily effluent from microbial oil production, rich in glycerol and free fatty acids that can replace pure carbon sources, though its high lipid content may require emulsification in a 5-day static setup.	28 °C, static, 5 d	0.63	[42]
<i>Gluconacetobacter xylinus</i> ATCC 10245	Crude distillery effluent is unconditioned waste from spirit production, containing ethanol	Static	10	[43]
<i>Gluconacetobacter oboediens</i>	Crude distillery effluent is unconditioned waste from spirit production, containing ethanol, residual sugars and minerals; simple filtration is sufficient to support an 8-day static BC fermentation.	30 °C, static, 8 d	8.2	[44]
<i>Gluconacetobacter xylinus</i>	Crude glycerol from biodiesel plants contains ~70–80% glycerol plus methanol and salts; after minimal purification it serves as an economical carbon source for 7-day static BC production.	30 °C, static, 7 d	12.4	[45]
<i>Komagataeibacter xylinus</i>	Sugarcane straw is the fibrous residue after harvest; dilute-acid or enzymatic pretreatment releases hemicellulosic sugars over a 15-day static culture, yielding moderate membrane growth.	30 °C, static, 15 d	5.0	[46]
<i>Komagataeibacter saccharivorans</i>	Crude distillery effluent, similar to other spirit wastes, provides residual sugars and minerals after simple clarification, enabling a 7-day static cellulose biosynthesis.	30 °C, static, 7 d	1.32	[47]
<i>Acetobacter pasteurianus</i>	Tomato juice is rich in glucose, fructose, organic acids and carotenoids, offering a sterile, nutrient-dense medium for 7-day BC production without supplementation.	30 °C, static, 7 d	7.96	[48]
<i>Gluconacetobacter xylinus</i>	A blend of sugar-beet molasses and cheese whey combines high sucrose and lactose levels with proteins and minerals, delivering a balanced carbon-nitrogen medium for a 14-day static culture.	28 °C, static, 14 d	18.6	[49]
<i>Komagataeibacter xylinus</i>	Mixed kitchen waste (vegetable and starch scraps) is homogenized and sterilized to yield a complex organic medium; over 15 days in static culture it generates moderate cellulose yields.	30 °C, static, 15 d	2.1	[50]

Continuation of the table

Microorganism	Low-Cost Substrate	Cultivation Conditions	BC (g/L)	References
<i>Gluconacetobacter xylinus</i>	Crude glycerol, identical to 2018 feedstock, again validated as a low-cost carbon source for a 7-day static culture, though yield can vary with glycerol purity.	30 °C, static, 7 d	2.96	[51]
<i>Gluconacetobacter xylinus</i>	A mixture of cashew apple juice and soybean molasses provides high sugar content plus trace nutrients; simple blending supports a 7-day static pellicle with good mechanical properties.	30 °C, static, 7 d	5.0	[52]
Symbiotic culture of bacteria and yeast (SCOBY)	Acerola juice is rich in vitamin C, simple sugars and organic acids; when fermented by a mixed bacterial – yeast consortium it yields a 10-day BC pellicle with enhanced antioxidant properties.	30 °C, static, 10 d	4.12	[53]

2.2 Genetic approaches

Genetic engineering has emerged as a powerful means to rewire and amplify BC biosynthesis, targeting both native producers and heterologous hosts. One strategy involves precise gene knock-outs to redirect metabolic flux: for example, deletion of the membrane-bound glucose dehydrogenase in *Komagataeibacter* resulted in a 2-fold boost in cellulose titers by preventing glucose diversion into gluconic acid [54]. Complementing loss-of-function mutations, promoter engineering and operon copy-number optimization have been used to elevate expression of the core cellulose synthase genes and their accessory factors. Buldum et al. (2018) demonstrated this in *Escherichia coli*, co-expressing the complete *bcs* operon alongside upstream glucanase under dual plasmid control, yielding a stable, reproducible chassis that lays the groundwork for further pathway refinement [55].

Building on these foundations, modern workflows integrate omics-guided metabolic flux analysis to pinpoint bottlenecks in precursor supply. Through ¹³C-labeling experiments and constraint-based modeling, researchers have identified limiting NADH regeneration and GTP availability as critical constraints, subsequently engineering overexpressed transhydrogenases and guanylate kinase to relieve these flux imbalances [56]. CRISPR interference platforms now enable fine-tuning of competing pathways – for instance, transient repression of phosphogluconate dehydratase channels more carbon toward UDP-Glc, the immediate substrate for cellulose synthase, yielding up to a 1.8-fold increase in BC in pilot bioreactors [57].

Adaptive laboratory evolution under selective pressures has been paired with whole-genome sequencing to isolate naturally occurring mutations

that confer both higher BC productivity and enhanced stress tolerance [58].

2.3 Co-culture approaches

Co-culture strategies have emerged as a versatile toolkit for amplifying both the yield and functionality of BC by leveraging metabolic complementarity among different microbes. In the pioneering work by Seto et al. (2006), co-cultivation of *Gluconacetobacter xylinus* st-60-12 with *Lactobacillus mali* st-20 in a 4% corn steep liquor (CSL)/sucrose medium yielded a threefold increase in BC production compared to monocultures [59]. Expanding on lactic acid bacteria partnerships, Jiang et al. (2023) demonstrated that pairing *Komagataeibacter nataicola* with *Lactobacillus fermentum* boosted titers from 2.5 to 13.8 g/L, a > 5-fold improvement, through enhanced $\beta(1\rightarrow4)$ -glucan synthase activity and organic acid-mediated flux activation [60]. Similarly, co-culture of *Bacillus cereus* with *K. xylinus* on corn stover enzymatic hydrolysate raised BC from 1.2 to 4.4 g/L, with acetoin and 2,3-butanediol from *B. cereus* driving increases in ATP and acetyl-CoA to fuel cellulose biosynthesis [60].

Beyond bacterial partnerships, exopolysaccharides (EPS) produced or added *in situ* can fine-tune BC's nanostructure and mechanics. Liu and Catchmark (2018) showed that supplementing *G. hansenii* cultures with 4–8 mg/L purified EPS from *Escherichia coli* ATCC 35860 integrated mannose-rich polymers into the cellulose network, boosting Young's modulus by 80% without altering crystallinity [61]. Brugnoli et al. (2023) engineered co-cultures of *Komagataeibacter* and hyaluronic acid-producing *Lactocaseibacillus* to fabricate BC–HA composites with BC yields reaching 3.4 g/L, embedding HA within the fibrillar matrix for potential biomedical scaffolds [62].

Cross-kingdom assemblies have further broadened co-culture possibilities. Caro-Astorga et al. (2021) established stable co-cultures of *Komagataeibacter rhaeticus* and *Saccharomyces cerevisiae*,

leveraging yeast-secreted enzymes to functionalize the cellulose during growth, enabling living BC materials with biosensing and biocatalytic functions [63].

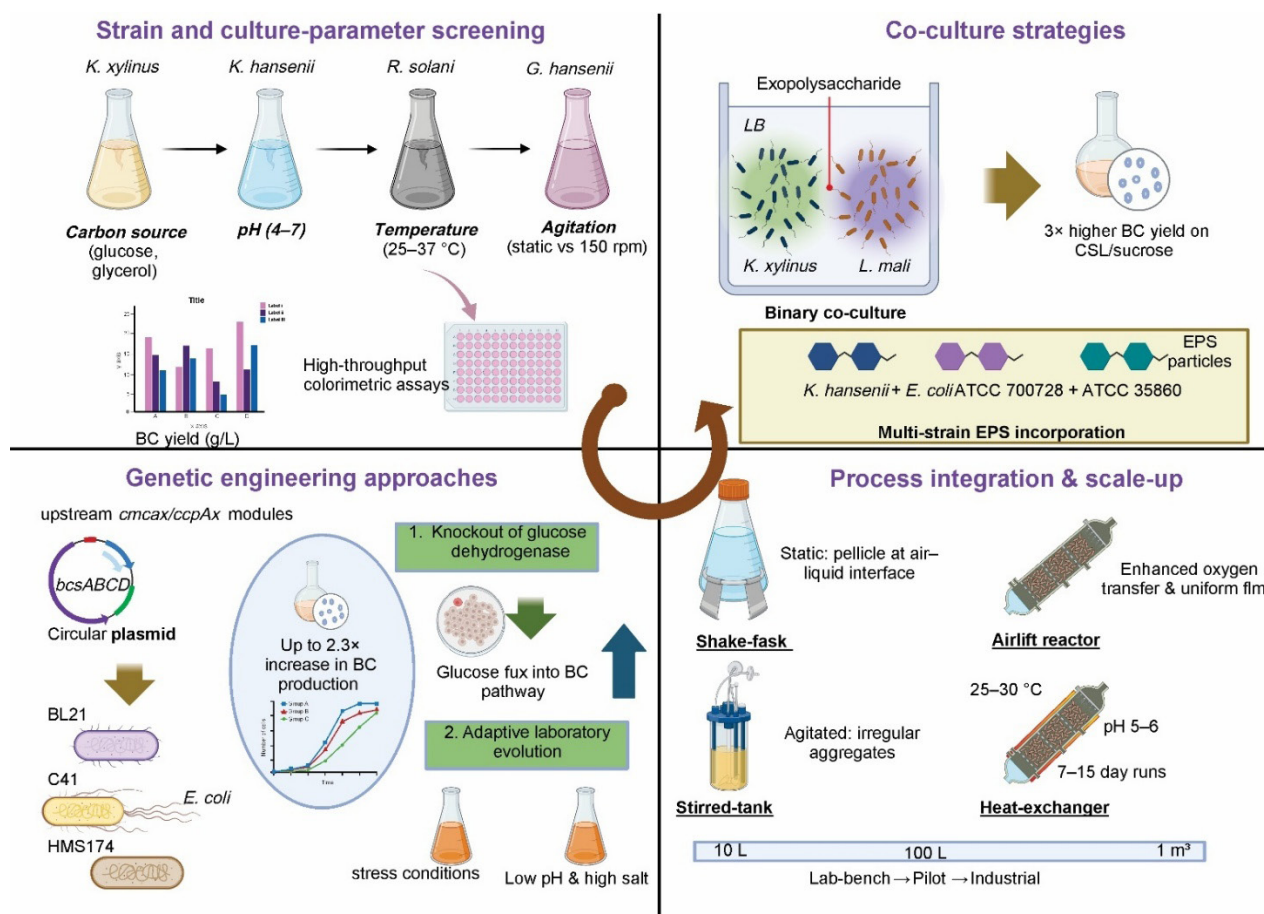


Figure 1 – Optimization of BC production. The workflow begins by screening diverse strains and culture parameters to pinpoint the highest-yielding BC producers. Next, targeted genetic modifications and adaptive evolution enhance their biosynthetic pathways and stress tolerance. Synergistic co-cultures exploit exopolysaccharide interactions to further boost cellulose output, and those optimized strains and conditions are then scaled from shake flasks into tailored bioreactor systems for industrial-grade production

The strategies summarized in Figure 1 highlight that successful enhancement of BC production requires a multilayered approach rather than reliance on a single intervention. Strain screening provides the foundational capacity for cellulose synthesis, but genetic engineering is often necessary to redirect carbon flux and improve pathway efficiency. Co-culture systems further expand metabolic capabilities by enabling complementary precursor supply or exopolysaccharide co-assembly. Ultimately, the effectiveness of these biological improvements depends on the integration of suitable cultivation modes and bioreactor configurations, particularly

with regard to oxygen transfer, pH control, and substrate economics. Thus, optimization of BC production is best understood as a coordinated workflow linking microbial design with scalable process engineering.

3. Main challenges and mitigation strategies

Despite the expanding toolbox of BC-producing microbes, several key challenges limit industrial scalability and economic viability. Table 2 summarizes these barriers alongside current mitigation strategies.

Table 2 – Key barriers and mitigation in BC production

Barrier	Impact	Mitigation strategies	References
High culture media Cost	HS medium ingredients are expensive; acidification leads to gluconic acid by-product.	Substitute with low-cost substrates; <i>in situ</i> pH control to minimize gluconic acid accumulation	[64, 65]
Low volumetric productivity	Static cultures limited to surface pellicle formation; shaking cultures suffer from shear-induced fragmentation.	Develop continuous or semi-continuous bioreactors with optimized aeration and mixing; use oxygen vectors to enhance dissolved oxygen	[66-68]
Strain variability and stability	Taxonomic reclassifications and undocumented strain IDs complicate reproducibility; plasmid-based genetic tools can be unstable.	Build standardized strain libraries with molecular barcoding; integrate cellulose operons chromosomally for genetic stability; employ CRISPR tools for precise genome edits	[68]
Scale-up complexity	Transitioning from flasks to industrial fermenters alters oxygen transfer, shear, and mass transfer characteristics.	Design modular scale-out systems; implement real-time process analytics; apply computational fluid dynamics to optimize reactor geometry	[69]
Sustainability and lifecycle	High water and energy consumption; limited end-of-life recycling pathways for BC composites.	Perform life cycle assessment (LCA) to guide process improvements; implement closed-loop water recycling; design compostable or enzymatically degradable BC materials	[70, 71]

High media cost

Research has demonstrated that agro-waste hydrolysates, such as sugarcane bagasse, fruit pomace, and crude glycerol from biodiesel production, can replace pure glucose at minimal yield penalties [8,18]. For instance, supplementation of spent sulfite liquor enabled *K. xylinus* to produce BC at 85% of HS yields, reducing raw material costs by over 60%. Coupling feedstock diversification with pH-stat fermentation can further suppress gluconic acid accumulation, maintaining metabolic flux toward cellulose synthesis [72-74].

Bioreactor design and process optimization

Bioreactor innovations have pivoted from static flasks to dynamic systems. Airlift reactors provide gentle mixing and enhanced oxygen transfer without damaging BC fibrils, while rotating disk reactors can produce tubular BC scaffolds with controlled porosity [75]. Advanced process control, leveraging online sensors and feedback loops for pH, dissolved oxygen, and redox potential, enables consistent product quality and higher volumetric productivity [76].

Genetic and synthetic biology

Chromosomal integration of the *bcs* operon under inducible promoters has stabilized high-yield phenotypes and allowed temporal control of cellulose synthesis [77]. Metabolic engineering to over-express UDP-Glc pyrophosphorylase and knock out competing pathways has increased precursor availability, resulting in up to 30% higher BC titers [78]. Heterologous expression in *E. coli* also facilitates

the incorporation of unnatural monomers for post-synthetic functionalization [79].

3.1 Future directions

As BC research matures, breakthroughs will increasingly hinge on interdisciplinary integration, melding microbial physiology with process engineering and advanced materials science. Below, we highlight five promising avenues that together can propel BC from laboratory curiosity to sustainable, high-value biomaterial platform.

Integrated biorefineries

Rather than viewing BC as a lone product, future processes should harness co-production of high-value metabolites, such as organic acids biosurfactants and nutraceuticals, in a single fermentation cascade. By coupling downstream separations to valorize each fraction, overall yield and revenue per unit feedstock can increase substantially. For example, feeding crude glycerol to a mixed *Komagataeibacter-Pseudomonas* consortium could generate BC pellicles while recovering rhamnolipids from the supernatant, enabling cost-effective glycerol remediation and dual-product biorefining [80].

3D printing and additive manufacturing

To meet the burgeoning demand for customized biomedical and wearable-electronics scaffolds, BC must be reformulated as a printable bioink with precisely tunable viscoelasticity. This will entail controlling nanofibril alignment and surface chemistry, through in-situ crosslinking agents or shear-directed assembly, to modulate shear thinning, yield stress and post-print shape fidelity. Advances in microex-

trusion printers and coaxial nozzles offer opportunities to embed live cells or conductive fillers directly during filament deposition, unlocking hierarchical, living constructs with integrated sensing or actuation functions [81].

Functional composite materials

Embedding functional moieties within the cellulose network during growth can create next-generation composites without post-fabrication coating steps. In-fermenter incorporation of monomers like aniline or pyrrole, followed by microbial or chemical polymerization, can yield BC-polyaniline or BC-polypyrrole films with intrinsic conductivity [82]. Seeding cultures with metal nanoparticle precursors plus mild reducing agents can produce uniform BC-metal nanocomposites for antimicrobial wound dressings or flexible electrodes. Stimuli-responsive additives, such as spiropyran or azobenzene derivatives, could confer light- or pH-switchable properties directly within the pellicle matrix [83].

Regulatory frameworks

To accelerate clinical trials and commercial uptake, the BC community must converge on standardized protocols for material characterization, mechanical testing and biocompatibility assays. Establishing ISO-aligned reference materials and round-robin interlaboratory studies will build confidence among regulators, enabling BC-based wound care products, implants and food additives to navigate approval pathways more efficiently [84].

Sustainability assessment

Rigorous LCA and techno-economic assessments are critical for guiding substrate choice, energy integration and downstream valorization. Comparing metrics such as global warming potential, water footprint and minimum selling price across feedstocks, from molasses and agro-residues to wastewaters, will identify sweet spots where environmental and economic benefits align. Incorporating renewable energy inputs and designing end-of-life strategies will ensure that large-scale BC production delivers genuine circular-bioeconomy outcomes [85, 86].

Conclusion

BC has progressed from a niche laboratory material to a leading candidate among next-generation biopolymers due to its exceptional physicochemical properties, including high mechanical strength, nanofibrillar purity, elasticity, and excellent biocompatibility. These attributes have enabled its integration into a wide range of fields, spanning biomedical applications such as wound dressings,

tissue engineering scaffolds, artificial skin substitutes, and controlled drug delivery systems, as well as environmentally conscious sectors such as biodegradable packaging, water purification membranes, and wearable or flexible electronic devices. Importantly, the ability to tailor BC's morphology and functionality through culture conditions, metabolic regulation, and composite formation provides a unique platform for manufacturing materials with application-specific performance. Despite these advantages, the widespread industrial deployment of BC remains limited by challenges in large-scale production, including relatively low volumetric productivity, high fermentation costs, sensitivity to shear stress, and difficulties in maintaining process reproducibility across reactors of increasing capacity. Recent advances in genetic engineering, adaptive laboratory evolution, and omics-guided metabolic optimization have begun to address these barriers by enhancing precursor supply, redirecting carbohydrate flux, and improving stress tolerance. Parallel progress in bioprocess engineering particularly continuous cultivation, airlift systems, and the valorization of agro-industrial residues as low-cost substrates contributes to cost reduction and sustainability. Looking forward, integrating BC production into circular biorefinery platforms, coupling biosynthesis with 3D bioprinting and additive manufacturing, and enabling in situ formation of multifunctional composites are likely to accelerate BC's transition from laboratory research to commercial-scale manufacturing. To support this transition, comprehensive life-cycle assessments, standardized material characterization protocols, and clear regulatory frameworks will be crucial in ensuring that BC fulfills its promise as a sustainable and industrially viable biomaterial.

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