Properties of bacterial cellulose developed from genetically stable FM833 bacterial strain for 30 generations via Kombucha tea

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Abstract The quality control of the bacterial cellulose (BC) production has been facing challenges due to the genetic stability of bacterial strains, which is often overlooked or underestimated. Thus, its commercialized application is limited. Therefore, a bacterial strain FM883 with a 16S rRNA sequence 97% identical to Komagataeibacter xylinus NBRC15237T was isolated from kombucha tea. Cultivation of FM883 was conducted in series to observe the morphology and BC yield among different generations from 1st generation to 30th generation. The results show that FM883 can efficiently produce BC in modified Hestrin-Schramm media at the 30th generation (163.5±0.3 g/L), which was even higher than the 1st generation (157.6±0.3 g/L). This indicated that FM883 has strong genetic stability. Furthermore, several characterizations of the BC indicated that the quality of the BC biosynthesized by FM883 was good with excellent thermostability. With such strong genetic stability, and properties, as well as sufficiently high consistency and high yield, BC biosynthesized by FM883 had demonstrated excellent production quality control, which is desired for commercial manufacturing.

Keywords Bacterial cellulose · Komagataeibacter xylinus · Morphology · Characterization · Genetic stability · Quality control

Introduction

Bacterial cellulose (BC) is a unique type of nanocellulose produced by microorganisms that has been thoroughly studied, mainly in terms of its biosynthesis and applications, since its discovery by Brown in 1886 (Brown 1886). It is known for its remarkable absorption capacity, biodegradability, biocompatibility, mechanical properties, and non-toxic features. Therefore, it is widely used in food industry (Lin et al. 2020), packaging film for food (Cazónand Vázquez 2021), tissue engineering (Bouhlooui et al. 2021), drug release (Adepu et al. 2021), medical treatments (Zhang et al. 2019), and wastewater treatment...
(Gholami et al. 2019). BC is biosynthesized by many bacterial strains such as *Gluconacetobacter* (Rubina et al. 2020), *Komagataeibacter* (Li et al. 2019), *Rhizobium* (Bhat et al. 2018), *Acetobacter pasteurianus* (Thakur et al. 2020), and *Azotobacter* (Quintana et al. 2021).

Despite its potential, BC could not completely replace other conventional materials for these applications. This is because the quality control of the BC production has been facing challenges due to the genetic stability of bacterial strains, which is often overlooked or underestimated. For example, studies conducted by Wu et al. (2010) demonstrated that the genetic stability of mutants of *G. xylinus* could only be maintained for five generations. Meanwhile, Deng et al. (2015) only studied the genetic stability of mutants of *G. xylinus* for ten generations. Moreover, the BC production yield is often affected significantly after several generations. For example, the yield of BC, which was synthesized by *Gluconacetobacter* sp. isolated from kombucha tea, was found to decrease by 72% from 1st generation to 10th generation (Li 2016). Furthermore, in the process of BC biosynthesis, bacterium resource, culture medium, fermentation methods and fermentation conditions could also affect the quality of the final product (Andriani et al. 2020; Du et al. 2020; Raiszadeh-Jahromi et al. 2020; Villarreal-Soto et al. 2021). Due to the formation of strong inter- and intra-hydrogen bonding after drying, the BC-based hydrogels have relatively low absorptive abilities (Chaiyasat et al. 2019). Ciecholewska-Juśko et al. (2021) presented a novel ex situ modification of BC polymer in order to improve its ability to absorb water after drying. However, its production is limited due to single production strain, low genetic stability, low yield of synthesis, and high cost of the culture media is needed industrialization (Quintana-Quirino et al. 2021). Therefore, it is still difficult to meet the needs of the application market for BC materials.

In order to solve these problems, seven distinct habitats of kombucha tea were used as screening sources to screen, isolate and to determine the genetic stability of high-yield BC strains. It should be noted that kombucha tea is a fermented tea that contains acetic acid bacteria (*Komagataeibacter*, *Gluconacetobacter*, and *Acetobacter* species) and yeasts (*Dekkera*, *Hanseniaspora* and *Zygosaccharomyces*) (Coton et al. 2017; De Roos and De Vuyst 2018). From these acetic acid bacteria, Li et al. (2019), Mohamed et al. (2019) and Zhang et al. (2018) were able to isolate *K. hansenii*, *Acetobacter pasteurianus* and *G. xylinus*, respectively from kombucha tea for the production of BC. In addition to genetic stability, the micro-optical structure, functional group characteristics of molecular surface, crystallinity and thermal stability of BC were characterized by scanning electron microscopy (SEM), transmission electron microscopy (TEM), Fourier transform infrared (FTIR) spectroscopy, X-ray diffraction (XRD), and thermogravimetric analysis (TG).

### Materials and methods

#### Materials

Various kombucha tea were purchased from Guangdong province, Shanxi province, Shandong province, Heilongjiang province, Beijing, Anhui province, and Xinjiang province. Glucose (AR, C₆H₁₂O₆, PubChem CID: 5739, CAS: 5996-10-1) was purchased from Sinopharm Chemical Reagent Co., Ltd. Yeast extract (BR, C₁₉H₁₄O₂, PubChem CID: 24,973,165, CAS: 8013-01-2), while agar (BR, C₁₄H₂₄O₉, PubChem CID: 71,571,511, CAS:9002-18-0) was purchased from Beijing Aoboxing Bio-tech Co., Ltd. Magnesium sulfate (AR, MgSO₄, PubChem CID: 24,083, CAS: 7487-88-9), dipotassium phosphate (AR, K₂HPO₄, PubChem CID: 24,450, CAS:7758-11-4) and ethyl alcohol (AR, CH₃CH₂OH, PubChem CID: 702, CAS:64-17-5) were purchased from Xilong Scientific Co., Ltd.

Hestrin-Schramm (HS) medium is a general culture medium for BC fermentation (Hestrin and Schramm 1954). The liquid culture medium that is used for fermenting BC was modified Hestrin-Schramm (MHS) media (Hestrin and Schramm 1954), which is conducive to BC production of FM883. This media contains 20 g/L glucose, 1 g/L K₂HPO₄, 5 g/L yeast extract, and 15 g/L MgSO₄. Liquid MHS medium was obtained by mixing with 2% ethanol (v/v) before fermentation and solid MHS medium was obtained by adding agar (20 g/L) to liquid MHS medium.

### Isolation and identification of bacterial strains producing BC

Biofilms from different kombucha teas were put into 250 mL beakers containing 100 mL liquid MHS medium and cultured at 30 °C for 7 days. The habitat
of kombucha tea producing the thickest BC was used for downstream cultivation. This optimum fermented liquid was cultured on solid MHS medium at 30 °C for 3 days, after which the strains were selected and sub-cultured in liquid MHS medium at 30 °C for 7 days. Finally, one strain (FM883) producing the thickest BC pellicle was selected for subsequent analysis.

The morphological, physical, and biochemical analysis of strain FM883 were carried out at the China Center for Type Culture Collection. The colony configuration and cell morphology were evaluated using SEM and TEM. The physiological and biochemical characteristics were investigated by growth in the presence of D-glucose, D-ribose, caprate, D-glucose of 5-keto-D-gluconate, glycogen, rhamnose, N-acetylglucosamine, saccharose, maltose, L-arabinose, galactose, mannose, D-xylose, glucose, inositol, esculin, trehalose, melibiose and D-fucose as carbon source. The 16S rRNA sequence analysis was conducted via DNA extraction, PCR amplification, cloning, and sequencing of 16S rRNA by Biosune Corporation (Shanghai, China).

Cultivation and harvest of BC was performed as followed, whereby strain FM883 was incubated in MHS medium at 30 °C for 7 days. Firstly, the BC pellicles floating in the medium were picked out and washed with ultrapure water thoroughly to remove the residual medium and other impurities. Next, the BC pellicles were boiled in 0.1 mol/L of NaOH for 30 min to eliminate microbial cells until the BC pellicles were transparent. The BC pellicles were then neutralized with 0.5% acetic acid, after which they were washed with ultrapure water repeatedly until the pH was 7.0. Finally, the wet BC pellicles were grounded (Retsch GM 200, Germany) and were freeze-dried. These BC pellicles were stored for subsequent analysis.

Genetic stability of strain FM883

The stability of strain FM883 was tested by cultivation on a solid MHS plate at 30 °C for 2 days as the 1st generation, whereby single colonies were selected and inoculated onto solid MHS plates which were then incubated at 30 °C for 3 days as the 2nd generation. This process was repeated until the 30th generation was achieved and the 1st, 5th, 10th, 15th, 20th, 25th, and 30th generation strains were characterized by TEM conducted by the China Center for Type Culture Collection. In addition, the 1st, 5th, 10th, 15th, 20th, 25th, and 30th generation strains were incubated in liquid MHS at 30 °C for 7 days, after which the BC was harvested and weighed to calculate the yield and the pH value of the liquor was determined.

Characterization of BC

FT-IR analysis of BC: FT-IR tests of BC pellicles were conducted using a Vertex 70 series FT-IR spectrometer (Bruker Optics Co., GER) with the KBr pellet method at wavelengths of 400–4000 cm⁻¹ with resolution of 2 cm⁻¹. XRD analysis of BC: XRD analysis of BC was conducted using an Empyrean X-ray diffraction instrument (D/mx-RB, Japan). The X-ray generator was operated at 40 kV and 160 mA with a Cu Kα radiation source (λ = 0.15418 nm). The reflection angle (2θ) ranged from 10° to 50°, with scanning speed of 0.5°/min and step size of 0.04°. Thermogravimetric analysis of BC: A thermogravimetric curve of the sample was recorded using a TG 209F3 (NETZSCH). The sample was heated in alumina pans at 30–800 °C under 100 mL/min nitrogen atmosphere at a heating rate of 10 °C/min. The sample mass was 9.5 mg.

Microstructure analysis of BC: SEM of BC samples was performed using a Jsm-6380lv SEM under low vacuum at 15 kV. Additionally, the BC samples were coated with Au before examination. TEM analysis of BC samples was performed as follows: The BC was homogenized in ultrapure water and was sonicated to achieve good dispersion. Next, drops of BC were deposited onto a copper-discharged grid. The BC was then fixed with 2.5% glutaraldehyde, washed three times with phosphate buffer solution, negatively stained with 1% (wt) phosphotungstic acid, and dried. Finally, the sample was observed with a Hitachi HT7700 microscope operating at 80 kV.

Swelling rate of BC

BC was dried to constant weight (noted as W₀). Next, the dried samples were soaked in ultrapure water at room temperature for 1, 2, 4, 6, 8, 26, 28, 32, 48, 50, 51, 53, 55, 103, 144, 150, and 156 h. After that, their surfaces were dried with filter paper, and the samples were weighted (noted as Wᵢ). The swelling rate (SR)
was calculated by the following equation (Deng et al. 2021):

\[
\text{Swelling rate (SR)} = \frac{W_1 - W_0}{W_0} \times 100\%
\]  

(1)

Results and discussion

Microorganism isolation and identification

The best BC producing strain (FM883) was isolated from the fermentation broth of kombucha tea obtained from Guangdong province. The strain was identified based on morphological, molecular, physical, and biochemical analyses. As shown in Fig. 1a, the observed colonies had a smooth surface, creamy white in color, regular edges, and raised elevation in the center of the colony. As shown in Fig. 1b–d, most of the cells were small ellipses with a short rod shape that occurred in single or in pairs. In addition, cells were about 0.83–1.46 µm in width and 1.03–2.31 µm in length (Fig. 1b). Interestingly, strain FM883 could secrete BC (Fig. 1c), and the surface of the cells was covered with a translucent BC layer (Fig. 1d).

The 16S rRNA sequence of strain FM883 was 1412 bp, and it shared 97% homology with strain Komagataeibacter xylinus NBRC15237T (Fig. 2). This indicated that strain FM883 is belonged to the Komagataeibacter group. Komagataeibacter was separated out from Gluconacetobacter in 2012 (Yamada et al. 2012), and is currently studied as an effective BC producer (Picheth et al. 2017). This strain has been preserved at the China Center for Type Culture Collection under preservation number CCTCC M 2019127. The 16S rRNA gene of strain FM883 was deposited in GenBank under the accession number MW757206.

The physiological and biochemical characteristics of FM883 are shown in Table 1. It was found that this strain could utilize many materials as carbon source. Moreover, it utilized L-arabinose, galactose, mannose, D-xylose, glucose, inositol, esculin, trehalose, melibiose or D-fucose as a carbon source to produce acid. Yet, there was one slight difference between the physiological and biochemical characteristics of FM883 and those of the strain described in Bergey’s Manual of Systematic Bacteriology (G. xylinus). G. xylinus is able to oxidize amino acids, but FM883 was not able to oxidize L-alanine, L-histidine, L-serine, or L-proline. Therefore, K. xylinus FM883 may be a new isolate of G. xylinus.

Fig. 1 Morphology of strain FM883. a Colonies without magnification, b 1000× magnification, c SEM analysis of 1st generation cells, d TEM analysis of 1st generation cells
Genetic stability

The results of TEM analysis of the 5th, 10th, 15th, 20th, 25th, and 30th generations of strain FM883 are shown in Fig. 3. A translucent BC layer covered the surface of strain FM883 cells in these images, similar to the 1st generation (Fig. 1d). The pH value at the end of fermentation was 2.8 for all generations. In addition, the concentration of total bacteria in the fermentation broth was more than $10^6$ cfu/mL for all generations, indicating good activity of strain FM883. As shown in Fig. 4, the BC yield of FM883 at the 5th, 10th, 15th, 20th, 25th, and 30th generation was 157.3 ± 0.6, 133.4 ± 0.9, 127.6 ± 1.2, 148.5 ± 0.6, 136.5 ± 0.4, 140.3 ± 1.6, and 165.3 ± 0.3 g/L, respectively, whereby the coefficient of variation was 9.3%.

This indicates that FM883 has strong genetic stability with sufficiently good consistency at such coefficient of variation (Liu et al. 2022), even after 30 generations. It should be noted that only a handful of studies were focused on genetic stability of bacteria strain on the production of BC. For example, by comparison with our work, the coefficient of variation for BC yield from G. xylinus mutants synthesized by Wu et al. (2010) at some conditions were 2.38–37.85%. Deng et al. (2015) was also able to achieve similar consistency by producing BC via mutants of G. xylinus, albeit with significantly lower BC yield at 14.9–15.8 g/L. Despite their consistencies were better than ours due to lower coefficient of variation values, it is not known whether it can be maintained beyond 10 generations, as they were produced only in 5

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**Fig. 2** Neighbor-joining phylogenetic tree of FM883 based on 16S rDNA sequences. Bootstrap values above 50% are shown at the branching points.

**Fig. 3** The 5th (a), 10th (b), 15th (c), 20th (d), 25th (e), and 30th (f) generation of strain FM883 cells through TEM.
generations and 10 generations, respectively up until then. Thus, it is not clear whether BC produced from *G. xylinus* has the potential to be commercialized. However, we managed to achieve beyond 10 generations, and the BC yield was able to be maintained at high amount with sufficient consistency even after 30 generations. Additionally, the BC yields produced by strain FM883 was relatively higher than many reported works tabulated in Table 2. For example, the BC yield was higher than those of *A. xylinum* (3.8–59.4 g/L) (Jagannath et al. 2008) and *K. hansenii* (30 g/L) (Kumbhar et al. 2015). It should be possible to optimize the culture medium and culture conditions or to add other substances such as acetate buffer to further improve the yield of BC and taste quality of fermentation broth of FM883 (Bilgi et al. 2016; Kuo et al. 2016). These findings demonstrated that strain FM883 is not only capable of producing BC with sufficiently good consistency even after 30 generations, but is also capable of producing high yield of BC. Hence, it has huge potential to be commercialized.

Characterization of BC

The FT-IR spectra of BC produced by strain FM883 in static conditions are shown in Fig. 5a. The peak at
3413 cm$^{-1}$ is a characteristic absorption band generated by the stretching vibration of O–H. The peak at 2924 cm$^{-1}$ is attributed to the $\text{-CH}_2\text{-}$ stretching vibration, while the peak at 1647 cm$^{-1}$ is corresponding to the stretching vibration of $\text{C}=\text{O}$. Meanwhile, the peaks at 1158 cm$^{-1}$ are attributed to the stretching vibration $\text{C–O–C}$ of 1,4-β glycoside pyranose ring. The peak at 1112 cm$^{-1}$ is corresponding to the monomer of a polysaccharide of C–O or C–C. The peak at 1057 cm$^{-1}$ is attributed to the $\text{C–O–C}$ pyranose ring skeletal vibration. These results were similar to those reported by Gayathri and Srinikethan (2019).

Cellulose generally consists of two crystalline phases, namely triclinic cellulose $\text{I}_\alpha$ and monoclinic $\text{I}_\beta$. The ratio of $\text{I}_\alpha$ to $\text{I}_\beta$ depends on the cellulose source and culture condition. In BC, $\text{I}_\alpha$ value is always greater than $\text{I}_\beta$ (Hosseini et al. 2018). The XRD pattern of BC produced by strain FM883 is shown in Fig. 5b. There are three distinct peaks at 14.5°, 16.8°, and 22.6° ($2\theta$), whereby the three main peaks for the $\text{I}_\alpha$ one-chain triclinic unit cell have Miller indices of (100), (010) and (110) according to French (2014). The standard curve of cellulose $\text{I}_\alpha$ was shown in the lower part of Fig. 5b. In order to clarify the structure of BC more clearly, the peaks of BC were compared with those of $\text{I}_\alpha$ and $\text{I}_\beta$ in supplementary file “profile fitting report”, whereby the standard peak (110) of cellulose $\text{I}_\alpha$ and the standard peak (200) of cellulose $\text{I}_\beta$ were used for semi-quantitative calculation. The fitting results showed that alpha accounted for 93% and beta accounted for 7% (The detail was shown in “profile fitting report”), which further confirmed that the overall structure of BC is $\text{I}_\alpha$. The crystallinity of cellulose imparts stiffness to fibrils and ribbons (Ruan et al. 2016), whereby the crystallinity of BC was determined to be 48.71%. The crystallinity of BC was found to be 41.45%, 38.76%, and 56.19% by Raiszadeh-Jahromi et al. (2020), 67% by Kumbhar et al. (2015), 77.5% by Abdelraof et al. (2019), 76.2% to 87.3% by Díaz-Ramírez et al. (2021), and 80.2% by Gayathri and Srinikethan (2019). The crystallinity variation was due to different culture medium in these studies. As a result, cellulose rearrangement was affected, thereby affecting the crystallinity (Hosseini et al. 2018).

The thermogravimetric (TG) and derivative thermogravimetric (DTG) curves for BC produced by strain FM883 are shown in Fig. 5c. There were three main weight losses. The first weight loss occurred from room temperature to 200 °C, with 13.62% of the total mass was lost. This weight loss was due to membrane dehydration or evaporation of surface water. The second weight loss, which occurred from 200 °C, was due to decomposition processes such as depolymerization and breakdown of de-hydrocellulose into gases (water, carbon monoxide, and carbon dioxide) (Rubina et al. 2020). The maximum decomposition temperature was at 330.6 °C, and the DTG was 5%/min. The third weight loss began at 380 °C and was due to calcination. The maximum decomposition temperature was at 442.1 °C, and the DTG was 1.4%/min. This weight loss was determined to be 70.52% at 620 °C, and the weight loss was found to decrease further by 4.27% only as the temperature approached 800 °C, which led to a residue rate of 25.21%. The peaks of DTG were of negative spikes, indicated that the test process was endothermic. The results of TG and DTG analysis indicated that the synthesized BC exhibits high thermal stability (Rezaei et al. 2020).

The results of SEM and TEM analysis of BC produced by K. xylinus FM883 in MHS media are shown in Fig. 5d and e, respectively. An architecture structure of BC matrices was observed at a magnification of $\times6000$. The average diameter of BC ribbons was determined to be within 10 and 70 nm. This was similar to the results reported by Chen et al. (2017).
and Kumar et al. (2021). The close-knitted network structure of BC from FM883 suggested that FM883 doubled the number of microfibril-synthesizing sites prior to division and both parent and daughter sites were active just before division. This resulted in the synthesis of a microfibrillar ribbon of constant dimensions. The size of the ultrastructure of BC has been shown to be a critical factor in determining the unique properties of reticulated BC (Rezaei et al. 2020).

Fig. 5  The FT-IR spectra (a), XRD pattern (b), TG and DTG pattern (c), SEM (d), and TEM (e) of BC produced by strain FM883
Swelling rate

The swelling rate is one of the important indicators for evaluating the performance of BC. The swelling rate of BC was shown in Fig. 6a, and it was found that the maximum swelling rate of BC was 4162.74 ± 12.74%. The adsorption dynamics can be described by the following equations (Wan et al. 2009):

\[ \frac{M_t - M_0}{M_e - M_0} = K t^n \]  
\[ \ln\left(\frac{M_t - M_0}{M_e - M_0}\right) = \ln K + n \ln t \]

\[ SR = 4\left(\frac{D t}{h^2}\right)^{0.5} \]

\[ D = \pi k^2 h^2 / 16 \]

where \( M_t \) and \( M_e \) are the equilibrium and at time \( t \) mass of BC (g), respectively. \( M_0 \) is the dry mass of BC (g). \( D \) is the diffusion coefficient and “\( h \)” represents the sample thickness. \( K \) is the network structure parameter. \( t \) is the water absorption time; \( n \) is the swelling characteristic index. It should be noted that if \( n \leq 0.5 \), the diffusion of BC in water is categorized as Fickian diffusion; if \( 0.5 < n < 1.0 \), the diffusion of BC in water is categorized as non-Fickian diffusion. On the other hand, if \( n \geq 1.0 \), the diffusion of BC in water is attributed to macromolecular chain relaxation diffusion. Since the \( n \) value of BC in this work was determined to be 0.3610, which was less than 0.5, therefore the diffusion of BC in water is due to Fickian diffusion. The diffusion behavior was investigated by using Eq. (5). There was a linear relationship between \( SR \) and \( t^{0.5} \), as shown in Fig. 6b. The slope \( k \) of the fitting line was used to calculate the diffusion coefficient \( D \) of BC in water according to Eq. (6), and was determined to be 1.5490. Similar diffusion type was also obtained by Wan et al. (2009) and Hosseini et al. (2018).

Conclusion

*K. xylinus* FM883 was isolated from kombucha tea and deposited in GenBank under the accession number MW757206. Strain FM883 has good genetic stability over 30 generations. The BC yield at the 30th generation (163.5 ± 0.3 g/L) was higher than the 1st generation (157.6 ± 0.3 g/L) with sufficient consistent production yield even after 30 generation, demonstrating the strong genetic stability in FM883. In addition, the BC produced by strain FM883 demonstrated good quality, with excellent thermostability, and the crystal of BC was 48.71% crystallinity index. These findings demonstrated that strain FM883 is capable of high production of BC with good quality control with good material properties that is desirable commercially.

![Fig. 6](image_url) The swelling rate of BC (a) and the water absorption rate after fitting (b)
Conflicts of interest

The authors declare no conflicts of interest with respect to this manuscript.

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