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REVIEW ARTICLE

Mechanistic insights of *Cystobasidium slooffiae* JSUX1: Yeast-derived microbial fuel cells and conversion of organic wastes to electricity

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Abstract

The pursuit of sustainable energy from abundant and renewable waste biomass has positioned microbial fuel cells (MFCs) as a capable technology. While bacterial MFCs are widely studied, yeast-based MFCs offer advantages in safety, ease of handling, and broader substrate utilization. The recent discovery and characterization of the exoelectrogenic yeast *Cystobasidium slooffiae* JSUX1 have opened new avenues for direct biomass-to-energy conversion. This review synthesizes recent advancements in leveraging *C. slooffiae* JSUX1 for efficient electricity and hydrogen production from pentose sugars and raw lignocellulosic biomass. We delve into the unique extracellular electron transfer mechanisms employed by this strain, notably its secretion of riboflavin and the newly identified role of humic acid-iron complexes (Fe-HA) derived from biomass degradation. *C. slooffiae* JSUX1 MFCs achieved peak power densities up to ≈152 mW/m^2 and hydrogen yields ≈41 L/m^3 (with engineered anodes), roughly double the baseline values of 67 mW/m^2 and 16 L/m^3. We further analyze applied strategies for enhancing MFCs' performance through anode engineering, including yeast-induced reduced graphene oxide hydrogels and polyaniline nanofiber anodes. These anode modifications significantly improved anode conductivity, microbial adhesion, and interfacial charge transfer, leading to a dramatic boost in simultaneous power and hydrogen output. This review consolidates the mechanistic understanding of *C. slooffiae* JSUX1 and situates it within broader yeast-MFC research trends, outlining its potential as a new biocatalyst for developing waste-valorizing bioelectrochemical systems.

Keywords: Microbial fuel cells; Yeast; *Cystobasidium slooffiae*; Electricity; Biohydrogen; Extracellular electron transfer; Untreated lignocellulosic biomass; Xylose

1. Introduction

The global energy crisis and environmental concerns have accelerated the exploration of sustainable technologies that can valorize waste into energy. Microbial fuel cells (MFCs) represent a cutting-edge platform that directly converts the chemical energy stored in organic substances into electrical energy through the catalytic activity of exoelectrogenic microorganisms.[1-3] This process offers the dual benefit of renewable energy generation

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and simultaneous waste remediation.[4,5] Lignocellulosic biomass, such as agricultural residues (e.g., rice straw, wheat straw), is one of the most abundant renewable resources on Earth. In China alone, annual rice straw production is estimated at 900 million tons.[6] Conventionally, harnessing energy from this robust material requires intensive physical, chemical, or physico-chemical pretreatments to break down complex polymers such as cellulose, hemicellulose, and lignin into fermentable sugars, followed by microbial fermentation.[7,8] These pretreatment steps are often costly, energy-intensive, and can generate fermentation inhibitors, including furan derivatives and phenols, hindering microbial activity.[6,9] A significant challenge in the field has been to find microorganisms capable of directly degrading raw, untreated biomass and efficiently transferring the derived electrons to the electrodes.

Research has emphasized well-studied exoelectrogenic bacteria (e.g., *Shewanella*, *Geobacter*). These bacteria often utilize direct outer-membrane cytochromes and conductive pili (microbial nanowires) to achieve high power densities (hundreds of mW/m^2).[10-13] *Shewanella oneidensis* uses a hybrid strategy: It possesses outer-membrane cytochromes but also secretes flavin molecules (riboflavin and flavin mononucleotide) as endogenous mediators that act as soluble mediators, enabling mediated electron transfer (MET) over short distances and improving effective extracellular electron transfer (EET) under conditions when direct contact is limited.[12,14] *Geobacter sulfurreducens* primarily uses conductive pili and outer-membrane cytochromes for contact-dependent EET. This contact-based mechanism supports very high EET rates and is a major reason bacterial MFCs can achieve high power densities up to hundreds of mW/m^2 in lab-scaled MFCs.[11,15,16] However, the bacterial strains lack the necessary transporters and metabolic pathways to directly break down pentoses, such as xylose, in MFCs.

On the contrary, yeasts (i.e., *Saccharomyces cerevisiae*) are generally recognized as safe, robust, easy to handle, and fast-growing.[6,11,17] They can metabolize a variety of carbon sources and thrive under non-anaerobic conditions. The first attempts at yeast-based MFCs date back to early demonstrations where baker's yeast (*S. cerevisiae*) oxidized glucose to CO_2 in an anode chamber while an exogenous mediator (e.g., methylene blue, phenanthraquinone) transported electrons to the electrode.[18] Despite these promising features, yeast MFCs have consistently demonstrated inferior power densities, typically <10 mW/m^2, in comparison to bacterial systems.[6,11] Yeasts conventionally lack the outer-membrane cytochromes and conductive pili found in certain bacterial systems, and their thick cell walls impose an additional barrier to DET, which results in suboptimal conductivity and a deceleration in EET processes. This limitation necessitates dependence on soluble external mediators for effective electron transport (Figure 1).

The evolution of yeast-based MFCs has been marked by concerted efforts to overcome their inherent limitations. Initial systems primarily relied on the model yeast *S. cerevisiae* and required the addition of exogenous mediators, such as methylene blue or neutral red, to shuttle electrons from the cell to the anode, resulting in low power outputs due to the limited mediator turnover and mediator toxicity concerns.[11,18] Concurrent research efforts concentrated on sophisticated anode design, incorporating materials such as conductive polymers (i.e., polypyrrole [PPy] and polyaniline [PANI]) nanocomposite structures, and carbon-based materials (graphene, reduced graphene oxide [rGO]) to increase effective surface area, promote microbial adhesion, and reduce charge-transfer resistance. For example, a gold-nanoparticle/PPy modification of *S. cerevisiae* electrodes boosted power to ~23 mW/m^2.[11] Similarly, a PPy-modified *S. cerevisiae* fuel cell reached ~45 mW/m^2,[19] whereas unmodified cells often yield <10 mW/m^2.[11] These engineering interventions often improved current density and stability but did not fully eliminate the need for mediators or address the limited substrate range of many yeast strains. Moreover, genetic engineering strategies have also been explored to augment electron generation and flux within yeast cells.[18,20,21] Beyond *S. cerevisiae*, studies have examined alternative yeasts (e.g., *Yarrowia*, *Pichia*, and *Candida* species) for their distinct metabolite profiles, enzyme secretion, or tolerance to complex substrates.[20] Some of these species exhibit better tolerance to inhibitors or produce metabolites that function as endogenous electron shuttles; however, most naturally occurring yeasts lack both efficient pentose metabolism and robust native EET capability. Genetic modifications have been explored to improve intracellular electron availability or to promote secretion of electron-shuttling molecules, but such approaches are still in early stages for practical MFC applications.

Despite these advancements, a significant gap remained: the lack of a robust, multifunctional yeast biocatalyst capable of directly converting the complex polymers in raw, untreated lignocellulosic biomass into electricity. A significant advancement emerged with the identification of unique electrochemical activity in specific nonconventional yeasts capable of synthesizing their own redox mediators, thus reducing reliance on externally supplied compounds for their electrochemical processes. The recent isolation and characterization of *Cystobasidium slooffiae* JSUX1 (isolated from activated sludge) have challenged this paradigm.[22] The yeast *C. slooffiae* JSUX1 demonstrated a remarkable capability to utilize pentose

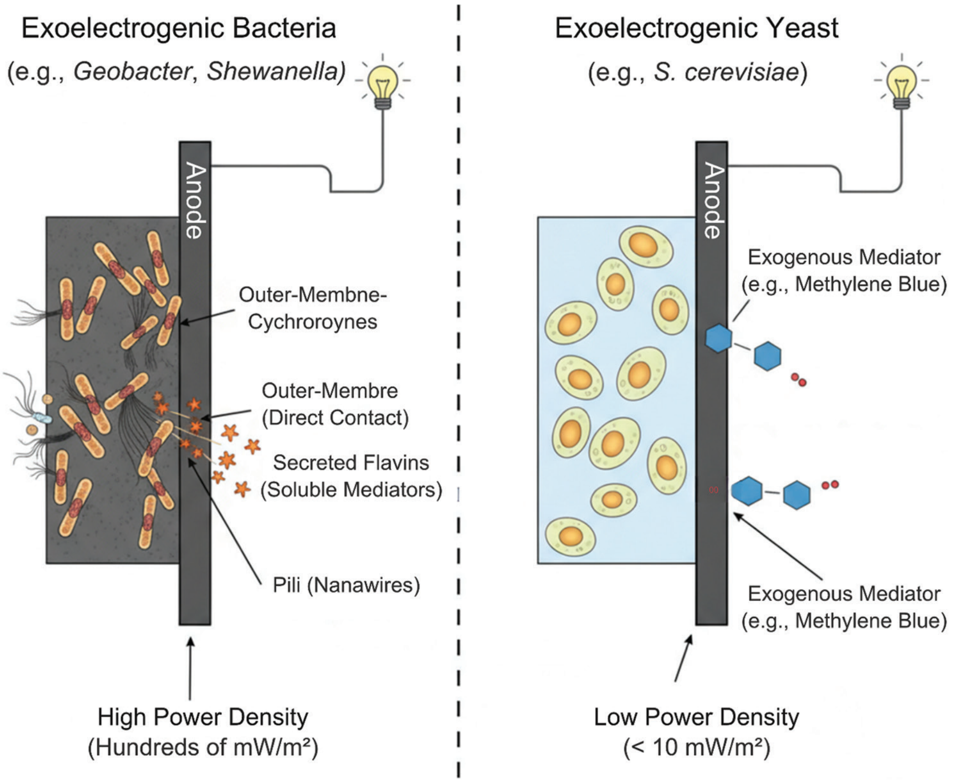

Figure 1. Comparison of electron transfer strategies in microbial fuel cells. Left panel: Bacterial extracellular electron transfer (EET): Model electrogenic bacteria (e.g., *Geobacter*, *Shewanella*) transfer electrons to the anode primarily via direct electron transfer (DET) through conductive pili (nanowires) and outer-membrane c-type cytochromes; *Shewanella* additionally secretes flavins, enabling short-range mediated electron transfer (MET). Right panel: Yeast EET: Conventional yeasts (e.g., *Saccharomyces cerevisiae*) lack conductive pili and outer-membrane cytochromes and therefore rely predominantly on soluble mediators (exogenous or endogenous) and engineered electrode interfaces to shuttle electrons to the anode. The schematic highlights why bacterial DET generally yields higher power densities.

sugars such as xylose and also to directly degrade raw lignocellulosic biomass for simultaneous electricity and hydrogen production.[6,23] These capabilities contrast with earlier yeast MFCs, which primarily used hexoses and mediators, marking a significant development in the field. This review aims to provide a mechanistic overview of the role of *C. slooffiae* JSUX1 in advancing yeast-based MFC technology. We analyzed its unique EET pathways, its distinctive enzymatic arsenal for biomass deconstruction, and how anode modifications synergize with this yeast to unlock performance in waste-to-energy conversion.

2. *C. slooffiae* JSUX1: A multifunctional exoelectrogenic yeast

2.1. Isolation and core capabilities

C. slooffiae JSUX1 was isolated from activated sludge and identified as a potent eukaryotic exoelectrogen.[22] The initial characterization revealed an exceptional capability to simultaneously produce bioelectricity and biohydrogen from xylose, the second most abundant sugar found in lignocellulosic hydrolysates, using double-chamber MFCs.[22] This directly positioned it as a valuable biocatalyst for biomass valorization, circumventing the common microbial inability to efficiently metabolize hemicellulose-derived pentose sugars. Previous studies on exoelectrogenic yeasts, such as *Pichia kudriavzevii* and *Candida melibiosica*, have demonstrated only negligible power output (single-digit mW/m^2) when utilizing glucose as a substrate.[20,24] A significant limitation for many yeasts, including the model eukaryote *S. cerevisiae*, is that they naturally lack the ability to produce compounds with redox-mediating capabilities, making their electroactivity dependent on the addition of exogenous mediators to facilitate EET processes.[24,25] *C. slooffiae* JSUX1 thus stands out by not only natively utilizing xylose for electricity production but also exhibiting inherent electroactivity through naturally secreting riboflavin, providing an endogenous MET route functionally analogous to *Shewanella's* flavin secretion but within an eukaryotic chassis.[6,26] Furthermore, it can leverage biomass-derived humic acid (HA)-iron (Fe-HA) complexes, creating a sophisticated, self-sustaining EET strategy that eliminates the need for external mediator additions.[6,22]

Functionally, these differences imply trade-offs, where bacterial DET (*Geobacter* spp.) affords the fastest per-cell EET and highest laboratory-scaled power densities, while MET strategies (*Shewanella* spp. and JSUX1) depend on mediator production and cycling but can operate with less stringent physical contact and can be more robust to complex substrates. *C. slooffiae* JSUX1's combination of endogenous mediator secretion and intrinsic lignocellulolytic activity is therefore significant as it reduces dependency on external mediators and upstream biomass pre-treatment, allowing direct use of low-cost, pentose-rich feedstocks (e.g., xylose from hemicellulose).

2.2. Enzymatic machinery for biomass degradation

A pivotal discovery was the strain's capability to directly attack raw biomass without any pre-treatment.[6] When inoculated on agar plates containing raw rice straw as the sole carbon source, *C. slooffiae* JSUX1 exhibited robust growth, confirmed by colony formation unit (CFU) assays (Figure 2A).[6] This growth is powered by its secretion of key lignocellulolytic enzymes: (i) laccase activity of 253.82 ± 3.09 U/L, crucial for breaking down lignin, the recalcitrant component of biomass, (ii) xylanase activity of 43.85 ± 0.30 U/mL, targeting hemicellulose, and (iii) cellulase activity of 0.33 ± 0.0054 U/mL, acting on cellulose polymers (Figure 2B).[6]

This enzymatic consortium enabled *C. slooffiae* JSUX1 to deconstruct the complex structure of rice straw into simpler sugars (primarily glucose) and organic acids (pyruvic, lactic, propionic) (Figure 3A and B), which subsequently served as fuel for electricity generation and cell growth within the MFC operation (Figure 3C and Table 1).[6]

Fourier-transform infrared (FTIR) and X-ray diffraction (XRD) analyses of the residual biomass confirmed the efficient degradation of amorphous regions of cellulose, hemicellulose, and lignin (Figure 3D and E).[6] FTIR analysis revealed distinct structural changes in rice straw before and after MFC-assisted hydrolysis. Characteristic aliphatic C–H stretching peaks (2,920 and 2,855 cm^{-1}) and hydroxyl (O–H, 3,270 cm^{-1}) and carbonyl (C=O, 1,730 cm^{-1}) groups exhibited reduced intensities after hydrolysis, indicating decreased hydrocarbons and lignin oxidation into phenolic/quinone groups. The aromatic C=C vibration (1,645–1,620 cm^{-1}) and carboxylic CO_2 stretching (1,420 cm^{-1}) also diminished, reflecting lignin degradation and cellulose breakdown by microbial enzymes. In addition, the disappearance of cellulose-associated C–H bending (1,370 cm^{-1}) and the attenuation of the C–O stretching band (1,030 cm^{-1}) confirmed efficient enzymatic hydrolysis of cellulose and hemicellulose (Figure 3D).[6,27,28] XRD analysis further supported these findings, showing a marked increase in crystallinity of the hydrolyzed straw compared with raw biomass, particularly in the intensities of the peaks corresponding to the (101), (101), and (002) lattice planes. This enhancement was attributed to the selective enzymatic removal of amorphous regions (amorphous cellulose, hemicellulose, and lignin), exposing crystalline cellulose.[6,29] The process also facilitated interfibrillar swelling and possible re-crystallization, where cellulose chains realigned into more ordered structures on enzymatic disruption of hydrogen bonds (Figure 3E).[6,30,31]

3. EET mechanisms

EET is the cornerstone of MFC operation. *C. slooffiae* JSUX1 employs and interacts with multiple EET pathways, making it exceptionally versatile (Figure 4).

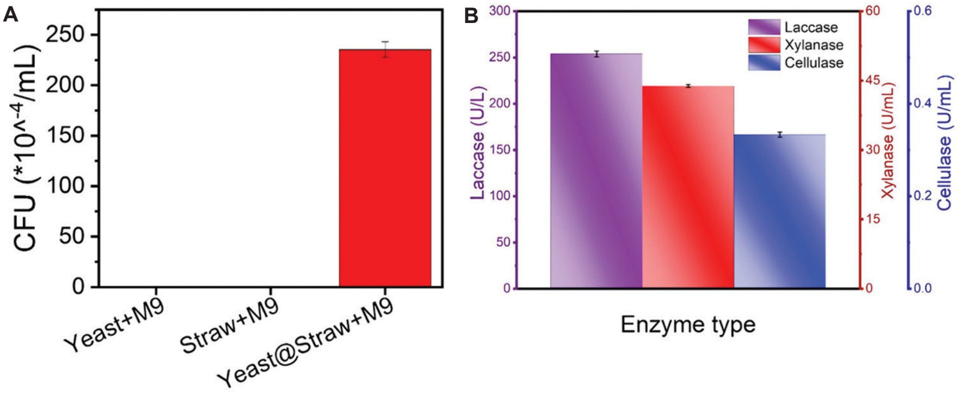

Figure 2. Growth on raw rice straw and lignocellulolytic enzyme activities of *Cystobasidium slooffiae* JSUX1. (A) Representative CFU plates after incubation on M9 agar containing 3 g/L raw rice straw (sole carbon source) vs. control plates (no straw or no inoculum) after 4 days, showing robust growth of JSUX1 on untreated biomass. (B) Measured lignocellulolytic enzymatic activities secreted by JSUX1 after 24 h: Laccase (reported 253.82 ± 3.09 U/L), xylanase (43.85 ± 0.30 U/mL), and cellulase (0.33 ± 0.0054 U/mL). These activities indicate the strain's capacity to depolymerize lignin and hemicellulose/cellulose *in situ* and underpin its ability to utilize raw straw as an electron and carbon source. Reprinted with permission from Moradian *et al.*[6] Copyright © 2024 Elsevier.

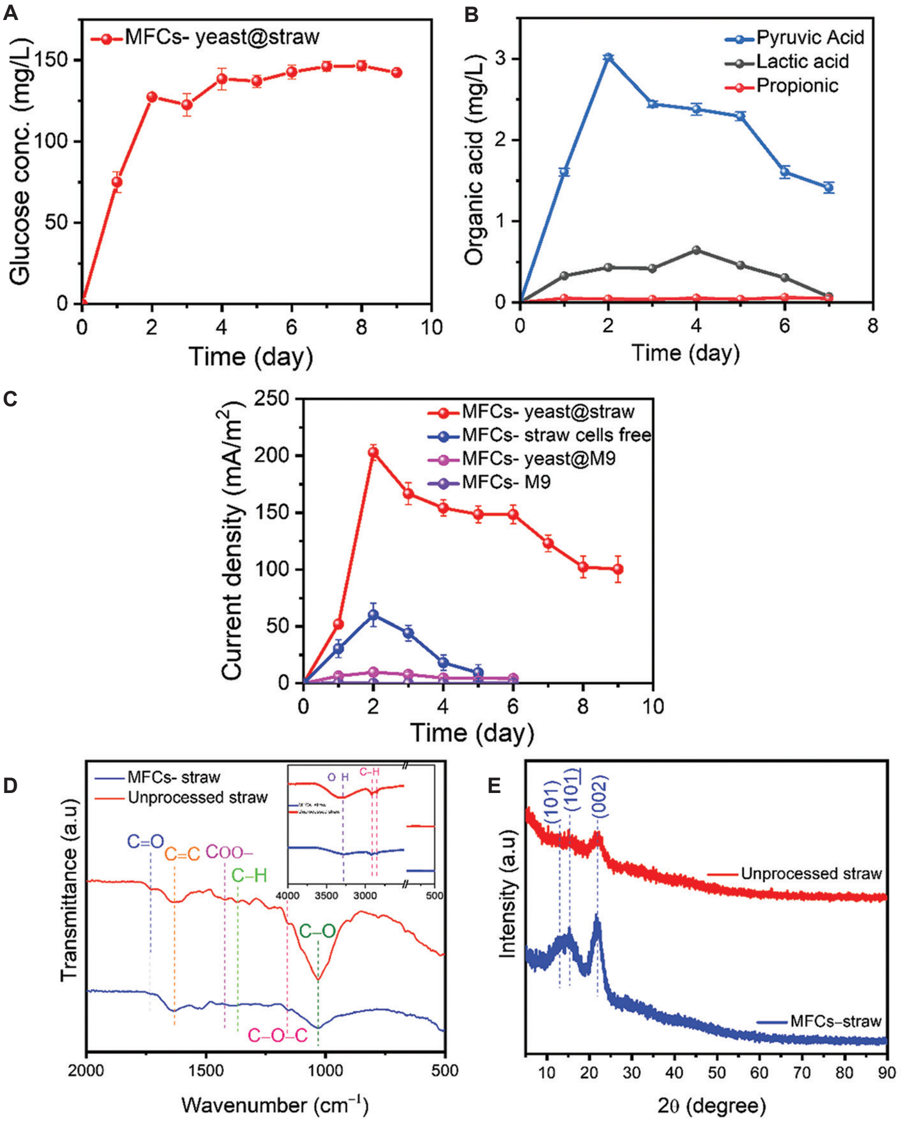

Figure 3. Chemical and electrochemical signatures of biomass conversion and MFC operation. HPLC profiles of (A) the evolution of glucose concentrations during MFC operation fed with raw rice straw and (B) organic acids (e.g., pyruvic, lactic, propionic acids) formed during enzymatic degradation and fermentation (retention time vs. concentration). (C) Current-time (I.T) curves for different electrolyte suspensions in MFCs. (D) FTIR spectra of raw rice straw (blue) and unprocessed straw (red), plotted as absorbance versus wavenumber (cm^{-1}), and (E) XRD diffractograms (intensity vs. 2θ) of raw rice straw after MFC discharge compared with unprocessed straw showing increased relative crystallinity after enzymatic removal of amorphous components. Reprinted with permission from Moradian *et al.*[6] Copyright © 2024 Elsevier.
Abbreviations: FTIR: Fourier-transform infrared; HPLC: High-performance liquid chromatography; MFC: Microbial fuel cell.

Table 1. Performance summary of *Cystobasidium slooffiae* JSUX1 MFCs with different substrates and anode modifications

Substrate	Anode	Power density (mW/m²)	Hydrogen production	Key mechanism	References
Xylose	Bare CF	67.1±1.98	16±1.1 L/m³	Riboflavin-mediated MET	22
Xylose	3D bio-rGO/hydrogel CF	152±2	~41 L/m³	3D conductive hydrogel, enhanced adhesion	23
Xylose	PANI/CF	119.35±3.27	25.82 mL/MFC chamber	PANI nanofibrillar network, improved R_{CT}	26
Raw rice straw	Bare CF	28.56±2.54	4.9±0.52 L/m³	Enzymatic degradation, HA/Fe-HA mediated MET	6

Abbreviations: CF: Carbon felt; HA: Humic acid; MET: Mediated electron transfer; MFC: Microbial fuel cell; PANI: Polyaniline; R_{CT}: Charge transfer resistance; rGO: Reduced graphene oxide.

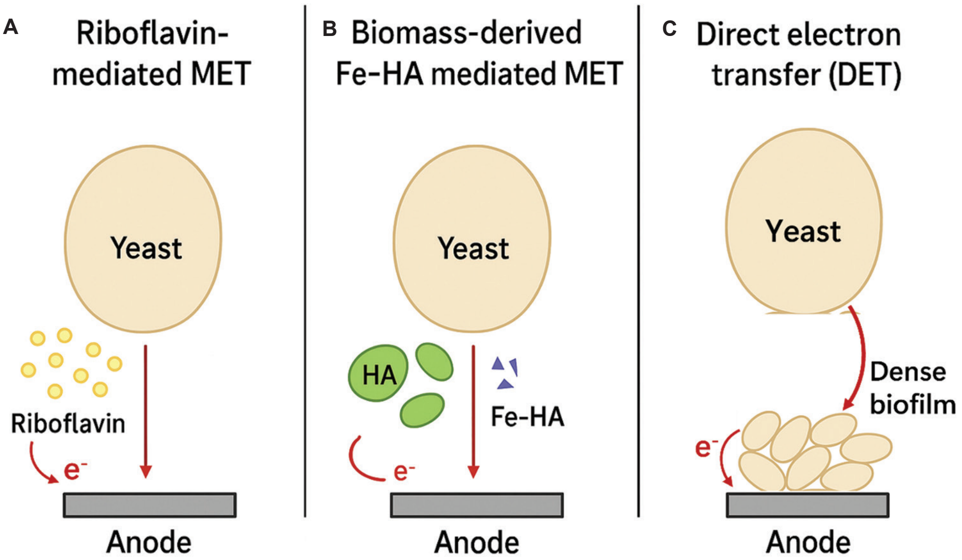

Figure 4. Comparison of the EET pathways in *Cystobasidium slooffiae* JSUX1-derived MFCs. The diagram integrates the three EET routes discussed in the text: (A) riboflavin-mediated MET, where JSUX1 secretes riboflavin that is reduced by cellular metabolism and re-oxidized at the anode; (B) biomass-derived humic acid or Fe–HA-mediated MET, where enzymatic degradation of raw biomass produces humic-like substances which complex with iron and act as PCET mediators between cells and electrode; (C) potential DET/DMET, where in the presence of highly conductive anodes (rGO, PANI) dense biofilms can form and enable contact-facilitated electron exchange (DET-like behavior).

Abbreviations: DET: Direct electron transfer; DMET: Direct-mediated electron transfer; EET: Extracellular electron transfer; MET: Mediated electron transfer; MFC: Microbial fuel cell; PANI: Polyaniline; PCET: Proton-coupled electron transfer; rGO: Reduced graphene oxide.

3.1. MET

Initial studies on xylose-fueled MFCs identified riboflavin as a soluble electron shuttle secreted by *C. slooffiae* JSUX1.[22] Cyclic voltammetry (CV) showed distinct redox peaks with a mid-point potential around −0.45 V (vs. SCE), characteristic of riboflavin.[22,32] This molecule facilitated MET, diffusing between the yeast cells and the anode, carrying electrons from cellular metabolic processes to the electrode surface.[22,26] Another innovative finding from the operation of MFCs on raw rice straw was the identification of a second, dominant EET pathway. CV analysis revealed a pair of strong redox peaks at −0.02 V (oxidation) and −0.27 V (reduction) versus SCE.[6] These peaks were present even in a straw-containing medium without inoculation, suggesting their origin from the biomass itself. The investigation identified HA and its complex with iron (Fe-HA) as the primary redox mediators, and HA was a natural product of biomass degradation. Its quinone groups could act as excellent electron shuttles, and when complexed with Fe^{3+}/Fe^{2+}, they created a highly efficient proton-coupled electron transfer (PCET) system (Figure 5).[6,33,34] The addition of exogenous HA or Fe^{2+} significantly amplified the redox peaks and drastically reduced charge transfer resistance (R_{CT}) as assessed by electrochemical impedance spectroscopy (EIS).[6]

3.2. Potential for direct electron transfer

While not yet conclusively proven, the formation of dense biofilms on developed anode materials (e.g., rGO hydrogels, PANI nanofibers) suggested the potential for direct contact-based EET.[23,26] The close physical proximity between the yeast cell walls and the conductive anode surface might have allowed for direct electron transfer through outer-membrane cytochromes or other conductive proteins, a pathway that may work in concert with MET mechanisms (Figure 6).

4. Anode modification for enhanced performance

The native inability of standard carbon-based anodes to support high-density *C. slooffiae* JSUX1 biofilms and facilitate efficient EET is a major bottleneck in yeast-MFCs. Research on *C. slooffiae* JSUX1 has successfully addressed this through anode engineering.

4.1. PANI nanofiber modification

An effective strategy involved synthesizing highly conductive PANI nanofibers using an ionic liquid dopant at room temperature and coating them onto the carbon felt (CF) anode.[26] Using this method, the resulting nanofibrillar PANI exhibited a significantly higher surface area of 46.474 m^2/g compared to earlier

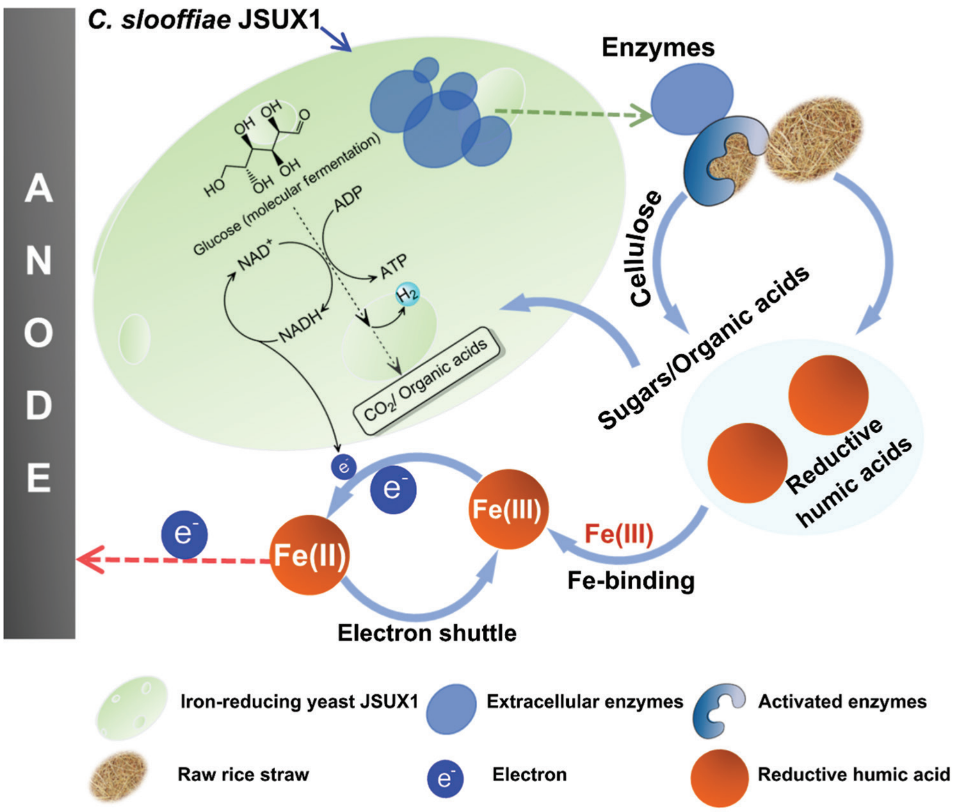

Figure 5. Schematic illustration of riboflavin and Fe–HA mediated EET in JSUX1 MFCs. This schematic shows the sequence: enzymatic hydrolysis of lignocellulose → release of fermentable sugars and organic acids → cellular oxidation producing electrons and protons; concurrently biomass degradation yields humic-like substances that complex with Fe (Fe–HA). The Fe–HA act as soluble redox mediator that shuttle electrons to the anode via PCET. Reprinted with permission from Moradian *et al.*[6] Copyright © 2024 Elsevier.
Abbreviations: EET: Extracellular electron transfer; MFC: Microbial fuel cell; PCET: Proton-coupled electron transfer.

reports on conventional PANI polymerization (33.6 m^2/g, 33.37 m^2/g, and 35.08 m^2/g).[35,36] The unique nanofibrillar structure (confirmed by SEM and BET analysis) formed an interconnected nanochannel network that provided a large, biocompatible surface for yeast cell attachment (Figure 7). This positively charged PANI also promoted electrostatic adhesion of negatively charged *C. slooffiae* JSUX1 cells. Furthermore, the modification enhanced anode conductivity and promoted the formation of a dense and electroactive biofilm. The PANI/CF anode improved the max power density to 119.35 ± 3.27 mW/m^2, which was 2.2 times higher than that of the bare CF anode (50.41 ± 6.9 mW/m^2). Hydrogen production also concurrently, along with electricity generation, increased by 1.6 times (25.82 ± 2.04 mL vs. 16.1 ± 2.58 mL) (Table 1).[26]

From a cost perspective, PANI is generally regarded as one of the most affordable conducting polymers, with commercial bulk prices for aniline monomer below USD8/10 kg and room-temperature chemical or electrochemical polymerization methods that are simple to scale.[26,37] However, maintaining the electrochemically active emeraldine salt form during prolonged MFC operation is challenging.[38] At positive anode potentials, PANI gradually over-oxidizes to the non-conductive pernigraniline form, leading to a permanent loss of conductivity and mechanical integrity.[39-41] Re-doping or periodic electrode replacement may thus be required in continuous reactors, adding maintenance costs and complexity at scale.

4.2. Yeast-induced rGO hydrogels

A unique, one-step biological anode modification strategy was developed where the yeast itself served as both a reductant and an assembly agent.[23] Graphene oxide (GO) nanosheets adsorbed onto a CF anode were reduced by *C. slooffiae* JSUX1 to form a 3D porous rGO hydrogel directly on the electrode surface.[23] In the yeast-induced hydrogel, the formation process involved the reduction and assembly of GO within the porous matrix of the CF, and the embedding of yeast within the forming hydrogel matrix (Figure 8). This process formed an interpenetrating network where the rGO is mechanically locked into the CF

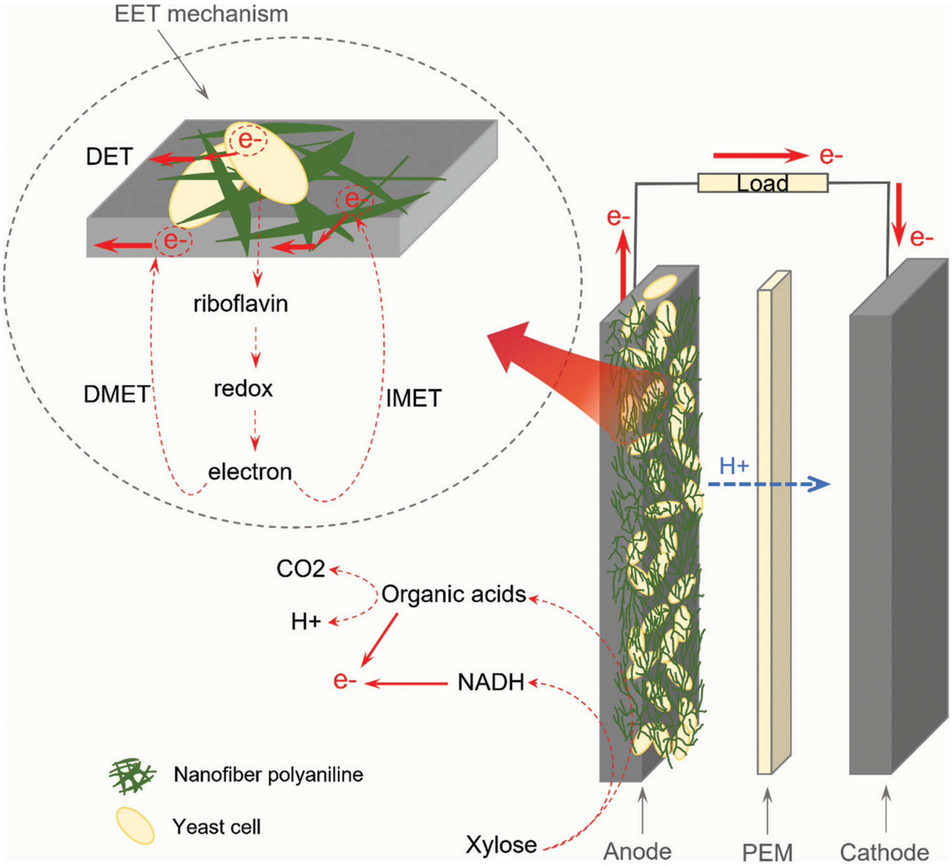

Figure 6. Conceptual illustration of improved EET pathways on conductive PANI/CF anodes. The figure contrasts three pathways operative when yeast interacts with a highly conductive PANI-modified carbon felt: DET—direct contact-based transfer when cells are in intimate contact with the conductive surface; DMET, short-range mediator cycling at the cell–anode interface facilitated by adsorbed mediators or surface redox sites; IMET, bulk soluble mediators (riboflavin, Fe–HA) shuttling electrons between planktonic cells and the electrode. Annotations indicate how PANI's high surface area, positive surface charge, and nanochannel structure promote biofilm formation, reduce R_{CT}, and enhance effective EET. Reprinted with permission from Moradian *et al.*[26] Copyright © 2022 Elsevier.

Abbreviations: CF: Carbon felt; DET: Direct electron transfer; DMET: Direct-mediated electron transfer; EET: Extracellular electron transfer; IMET: Indirect mediated electron transfer; PANI: Polyaniline.

structure, making delamination a far less significant issue compared to a coated polymer film.

This 3D structure provided a tremendous increase in specific surface area, facilitating superior *C. slooffiae* JSUX1 adhesion and biofilm formation. It also significantly enhanced the anode's electrical conductivity and capacitance. This self-modified bio-rGO/CF anode led to a 2.3-fold increase in maximum power density (152 ± 2 vs. 67 ± 2 mW/m^2) and a 2-fold increase in hydrogen production from xylose compared to a bare CF anode (Table 1).[23] EIS confirmed a dramatic 39-fold decrease in R_{CT}.

Although rGO anodes exhibit exceptional chemical and electrochemical stability under neutral pH and mild temperatures typical of MFC operation. The main limitation is cost, where even with recent advances in green and microbial reduction routes, producing high-surface-area rGO sheets or hydrogels remains considerably more expensive than CF or graphite materials (~USD 100–400/kg, depending on purity and processing route). In addition, large-area, defect-free hydrogel fabrication and uniform integration onto macroscopic electrodes are technically demanding.[42] Nevertheless, the long operational lifetime, structural robustness, and superior conductivity of rGO can offset some of these costs when system durability is considered over multiple cycles.[43]

5. Challenges and future perspectives

Despite the impressive progress in yeast-MFC research, significant challenges remain in translating laboratory success to larger scales and real-world applications. A central technical limitation is the intrinsic rate of enzymatic hydrolysis, where even with JSUX1's relatively

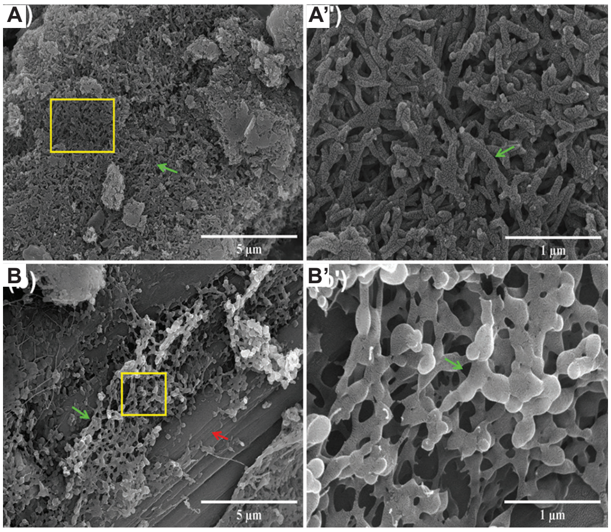

Figure 7. Morphology and electrode assembly of nanofibrillar PANI on CF (PANI/CF): (A, A') SEM of the synthesized PANI powder without PTFE binder showing nanofibrillar morphology; (B, B') PANI mixed with PTFE binder and coated on CF material to produce PANI/CF electrodes. SEM insets show the interconnected nanochannel network formed by nanofibrillar PANI that increases surface area and provides attachment sites for yeast cells. Green and red arrows (as marked on the panels) indicate representative PANI nanofibers and the underlying CF matrix, respectively; the yellow frames highlight regions shown at higher magnification. Reprinted with permission from Moradian *et al.*[26] Copyright © 2022 Elsevier.

Abbreviations: CF: Carbon felt; PANI: Polyaniline; PTFE: Polytetrafluoroethylene; SEM: Scanning electron microscopy.

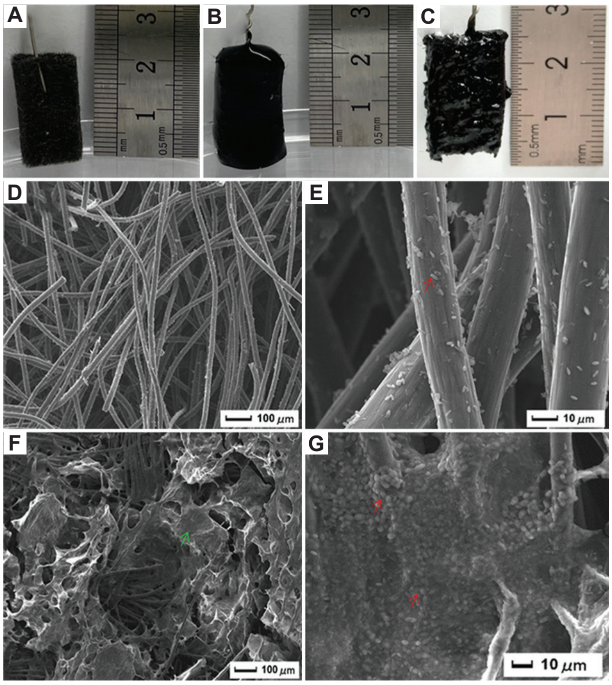

Figure 8. Yeast-induced bio-rGO/CF hydrogel: macroscopic photographs and SEM micrographs. (A-C) Photographs: Bare CF anode (A), CF with adsorbed GO (B), and CF after yeast-induced reduction and assembly into a 3D bio-rGO/CF hydrogel (showing the visually darker, monolithic hydrogel layer) (C). (D-G) The SEM images of bare CF anode (D and E) and bio-rGO/CF anode (F and G) after MFC discharge at two magnifications. Red arrows indicate yeast cells embedded in the hydrogel matrix; green arrows indicate rGO nanosheets. The bio-rGO/CF structure provides enhanced surface area, improved electrical connectivity, and mechanical locking of rGO into the CF scaffold. Reprinted with permission from Moradian *et al.*[23] Copyright © 2021 Elsevier.

Abbreviations: CF: Carbon felt; SEM: Scanning electron microscopy.

rich enzyme cocktail, conversion of untreated rice straw to fermentable monomers in batch experiments extends over several days. This slow hydrolysis increases MFC cycle times relative to feeding refined sugars or pretreated hydrolysates and reduces volumetric productivity in continuous or semi-continuous systems. Although power densities after the anode engineering have significantly improved, further enhancement is needed for them to be commercially viable, as scaling up MFCs often results in increased internal resistances and complexities in reactor design. The direct degradation of raw biomass, which removes the need for pretreatment, inherently occurs at a slower rate than using refined sugars or pretreated hydrolysates, resulting in longer cycle times and lower volumetric production rates.

Material durability and lifecycle costs are equally critical. PANI offers a low-cost route to boost anode conductivity and biotic adhesion, but the emeraldine salt form is vulnerable to over-oxidation at anodic potentials and can irreversibly convert to non-conductive pernigraniline, degrading its conductivity and electrocatalytic properties over time. However, for rGO, the economic implications of the precursor (GO) and the energy demands for its reduction processes are relatively high, though scalable reduction methods, thermal or chemical reduction, can be optimized to mitigate these challenges. In addition, graphene and its derivatives (rGO) are composed of sp^2-hybridized carbon, forming a very thermodynamically stable structure. They are chemically inert under the typical neutral pH and mild temperature conditions of MFCs, where they are not susceptible to electrochemical over-oxidation in the same way as PANI. The 3D rGO hydrogels are a monolithic, crosslinked carbon network. This material maintains its stability without significant swelling/shrinking thanks to strong van der Waals forces and π-π interactions between graphene sheets, making it structurally robust and resistant to physical disintegration.

Although the yeast-induced reduction method used for JSUX1 presents a unique, bio-catalytic route that could potentially lower energy inputs. However, considering industrial-scale MFCs for waste treatment, the balance between performance gains and the lifetime cost of the electrode materials becomes paramount, directing future research toward more robust, abundant, and low-cost carbon-based composites. PANI offers a low-cost but less stable option for short-term or disposable MFCs, whereas rGO provides a high-performance yet cost-intensive alternative suited to high-value applications or modular long-term systems. Future scaling strategies may focus on composite electrodes, combining low-cost carbons with small fractions of conductive polymers or graphene derivatives, to balance performance with manufacturability.

To move yeast-MFCs toward deployment, future research should prioritize system integration and hybridization with existing bioenergy and waste-treatment infrastructures. Concrete opportunities include:

(i) Biorefinery integration (cascade use of feedstocks): JSUX1 can be embedded within lignocellulosic biorefinery schemes where hemicellulosic (xylose-rich) streams are routed to MFC modules for direct electricity and hydrogen recovery, while cellulose-rich fractions proceed to enzymatic hydrolysis and fermentation for fuels or chemicals. This cascading use improves overall carbon valorization and reduces the need for harsh pretreatment on the fraction destined for the MFCs.

(ii) Agro-industrial wastewater treatment: Many agro-industries (pulp and paper, sugarcane processing, distilleries, olive mills) produce high chemical oxygen demand streams with residual soluble and particulate organics. Modular JSUX1-MFC units could act as pretreatment or polishing stages that recover energy (electricity, H_2) while reducing pollutant loads, enhancing the economics of onsite treatment.

(iii) Coupling with anaerobic digestion (AD): Hybrid schemes can be bidirectional: (a) MFC as a front-end partial hydrolysis/electron recovery step that extracts high-value electrons and reduces inhibitor loads before feeding residue to AD for methane; or (b) AD as a pretreatment producing soluble organics (volatile fatty acids, sugars) that boost MFC current density when targeted feeds are supplied. Such co-location enables energy cascading (electricity and H_2) and improves total energy recovery from a single feedstock.

(iv) Integration with microbial electrolysis cells (MECs) and photobioreactors: MFCs can be coupled with MECs to increase hydrogen yields where an applied low-voltage input is acceptable (e.g., surplus renewable electricity). Photobioreactors (algae) can supply oxygen for cathodic reactions, remediate catholyte effluent, or produce additional organics that feed the anode, forming an integrated photosynthetic-bioelectrochemical system.

(v) Co-culture and consortium strategies: Combining JSUX1 with bacterial exoelectrogens (e.g., *Geobacter*, *Shewanella*) may synergistically improve EET: bacteria provide fast DET pathways and conductive biofilms while JSUX1 contributes pentose utilization and lignocellulolytic activity. Co-culture arrangements should be explored in controlled continuous systems to manage competition, syntrophy, and stability.

To realize the integrations above, pilot demonstrations and standardized metrics are essential. Pilot designs could include modular continuous-flow MFC stacks fed by real process streams (e.g., hemicellulose liquor from a sugarcane refinery or wash water from a pulp mill) with parallel AD or MEC units to quantify combined energy yields, chemical oxygen demand removal, and operational stability over months. Important evaluation metrics should include areal power density (mW/m^2), volumetric hydrogen production (L/m^3), Coulombic efficiency, electrode lifetime (cycles or operational days to 80% performance), maintenance intervals, and a levelized cost of energy estimate for the integrated system.

Finally, we summarize key open research questions that will guide the next phase of JSUX1-based MFC development:

(i) What reactor configurations (single vs. stacked, flow-through, packed bed, 3D electrode assemblies) maximize both contact area and hydraulic throughput while minimizing internal resistance at scale?

(ii) How can anode materials be engineered as low-cost composites that preserve the conductivity and stability of rGO/PANI at dramatically lower material loading and manufacturing cost? What are practical recycling or refurbishment strategies for end-of-life electrodes?

(iii) How do JSUX1 enzyme secretion profiles and mediator production change over long-term continuous operation, and what strategies (process control, nutrient dosing, adaptive bioaugmentation) maintain stable performance?

(iv) What co-culture designs and control strategies enable synergistic cooperation between JSUX1 and bacterial electrogens without competitive collapse?

(v) What are realistic techno-economic and life-cycle assessments for integrated JSUX1 MFC modules (standalone or hybridized with AD/MEC/photobioreactors) processing agro-industrial streams at pilot and demonstration scales?

Addressing these questions with multidisciplinary efforts, combining microbiology, materials science, reactor engineering, and techno-economic analysis, will be essential to move yeast-based MFCs from promising laboratory demonstrations to robust components of circular bioeconomy infrastructures.

6. Conclusion

The discovery and development of *C. slooffiae* JSUX1 represent a significant leap forward in yeast-based MFC technology. This review has highlighted its unique multifunctionality: it is an efficient exoelectrogen, a prolific producer of biohydrogen, and a self-sufficient biocatalyst capable of secreting a suite of enzymes to directly deconstruct raw lignocellulosic biomass. Its EET strategy is sophisticated, utilizing both self-secreted (riboflavin) and biomass-derived (HA/Fe-HA) redox mediators to ensure efficient electron flux. When coupled with engineered anode materials, including yeast-induced 3D rGO hydrogels or nanofibrillar PANI, the performance of *C. slooffiae* JSUX1 MFCs was dramatically enhanced, showcasing the critical interplay between microbiology and materials science. This body of work not only provides mechanistic insights into a novel yeast biocatalyst but also establishes a robust framework for the development of efficient, sustainable, and waste-utilizing bioelectrochemical systems for the future bioeconomy.

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Conflict of interest

The authors declare they have no competing interests.

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