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Techno-economic assessment of single-cell protein production at industrial scale from a wide range of carbon sources

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ABSTRACT

Using aerobic fermentation, single-cell protein (SCP) can be produced from a wide range of carbon sources (C-sources), including glucose, glycerol, methanol, ethanol, and organic acids. The technical and economic performance of large-scale SCP production varies significantly with C-source, driven by differences in biomass yield, O_2 demand, and productivity, for example. To determine the preferred C-source, a techno-economic assessment for continuous SCP production in an industrial bubble column was performed for nine non-gaseous C-sources. This was based on a process model that included microbial kinetics, gas-liquid mass transfer kinetics, downstream operations, and a detailed cost analysis. Per C-source, dilution rate and aeration conditions were optimized to minimize the minimum selling price (MSP) of SCP. The results highlight C-source costs as the dominant MSP driver, with O_2 transfer rates strongly affecting capital and utility costs. At their current prices, glucose, glycerol, methanol and ethanol emerge as the most economically favorable C-sources, achieving MSPs of about 2.5 $/kg$_x$ due to high biomass yields and low C-source prices. Acetic acid exhibits an MSP of 3.2 $/kg$_x$ but, lactic, formic, glycolic and oxalic acids exhibit MSPs in the range of 7–20 $/kg$_x$ due to low biomass yields, high O_2 demand, and high C-source prices. Sensitivity analyses confirm that C-source price and biomass yield exert the strongest economic influence, while the electricity price and fixed costs have a more marginal effect. This work identifies promising candidates for further environmental and scale-up assessments, providing a framework to guide C-source selection and process optimization for SCP production.

1. Introduction

As the global population grows and dietary patterns shift toward protein-rich foods, the pressure on conventional protein production systems is intensifying. Traditional protein sources, particularly meat and dairy, require large amounts of land, water, and energy, and are responsible for a significant share of agricultural greenhouse gas emissions [1,2]. This creates an urgent need for alternative proteins that are both nutritionally adequate and environmentally sustainable. Single-cell protein (SCP), derived from microbial biomass such as bacteria, yeast, fungi, and algae [3], presents a promising solution. Specific microorganisms can be grown rapidly and at high yields using *i)* traditional agriculture-derived fermentation C-sources such as carbohydrates, ethanol and glycerol, *ii)* fossil C-sources such as methane, *iii)* biomethane, *iv)* products of electroreduction of CO_2 such as formic acid, acetic acid and methanol, or *v)* CO_2 in combination with H_2, the electroreduction product of water [4,5]. The use of gaseous substrates presents issues with scalability, safety and performance that are difficult and costly to mitigate, and they are left out of scope, as will be discussed later. Phototrophic growth on CO_2 is another option but is costly at industrial scale due to the need for illuminated bioreactors at very large production volumes. Therefore, we focus on chemotrophic growth of microbes on liquid and solid fermentation C-sources in traditional industrial bioreactors. Aerobic rather than anaerobic processes are considered to avoid low SCP yields and fermentation co-products.

Commercial industrial SCP production has been reported on the basis of carbohydrate, and on the basis of methane and methanol of fossil origin [6,7]. However, assuming the future availability of abundant renewably produced electric power for electroreduction of CO_2 and water, we wondered, like others [8–10] which C-source originating from electroreduction would allow industrial-scale SCP production at lowest costs and environmental impact. A systematic techno-economic

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comparison with sufficient details on bioreactor design and operation is lacking. Here, we will provide a framework for cost comparison. We use current C-source prices to compare carbon sources, although these are based on conventional rather than on electrochemical manufacturing platforms. Evaluating electrochemical production methods of C-sources is out of scope here. Still, we take into consideration that pure O_2, which is co-produced during electrochemical reduction of CO_2 or water, might be used instead of air for the aerobic SCP production. Our preceding study [5] presented a bioreactor model that allowed optimization of the operating conditions for continuous production of SCP from ethanol in a 600 m^3 bubble column. As the O_2 transfer capacity was rate-limiting, a higher O_2 transfer rate was achieved using pure O_2 rather than using air.

The aforementioned model [5] also allowed the calculation of the large cooling duty required, and guided us toward the option of using a modest ethanol feed concentration (e.g. 20–30 mass%) since 95 or 100 mass% ethanol would not be completely consumed at otherwise favorable operational settings. In this paper, we use the same bioreactor model to evaluate a range of C-sources besides ethanol that may be converted into SCP. Some of those, such as methanol, formic acid and acetic acid, can be generated by CO_2 electroreduction, but we also evaluate traditional C-sources such as glucose and glycerol, for comparison reasons. Not only are gaseous feedstocks out of scope, but also carboxylate salts (e.g. sodium acetate) for reasons that will be discussed later.

The aim of this work is to explore the influence of C-source on the economics of the SCP production process. A set of performance indicators for the fermentation is used, such as feed inlet concentration, conversion yield and bioreactor productivity. These directly influence capital and operational costs. The scale of the first part of the downstream process design will depend on the SCP concentration and the outflow rate from the bioreactor, but the final part of the downstream processing design to obtain crude, dry SCP will be largely similar for each C-source type as the plant output is set at 12 kt of SCP per year for each C-source. Per C-source, the minimum selling price is optimized by tuning key operational variables of the fermentation. This approach identifies the most promising C-sources for future SCP scale-up and suggests strategies for cost reduction.

2. Methodology

2.1. Microbial growth kinetics and stoichiometry

To obtain low SCP production costs, high SCP yields are important. Theoretically achievable yields will be discussed in Section 2.4, but for the base-case bioreactor design we focused on experimental yields. The maximum yields $Y_{x/s}^{max}$ of biomass (X) on C-source (S) were assumed to equal the highest experimental values reported for various microbial species in literature (shown in Table S1 in Supplementary file 1). The given references used growth rates of at least 0.15 h^{-1} at a temperature near to 30 °C and using minimal media with ammonia as nitrogen source. Using elemental balances and values of $Y_{x/s}^{max}$ the reaction stoichiometries were calculated. So, our approach chooses per C-source a different microbe, namely the microbe with the highest reported biomass yield on that C-source. The maximum uptake rates (q_S^{max}) and maintenance coefficients (m_S) were estimated using literature correlations [11] due to *i)* scarcely available experimental data and *ii)* their low influence on the technical performance of the bioreactor at high dilution rates [5]. The obtained values for q_S^{max} and m_S are summarized in Table S3 with the maximum biomass-specific growth rate (μ^{max}), which was calculated using the Pirt equation [11].

2.2. Model of the bioreactor and of the overall SCP production process

As mentioned, the design aims for a production capacity of 12,000 t/a of SCP. This is within the range used in this field. Like previously [5], the process uses a single bubble column bioreactor, continuously operating in steady-state for 330 days per year. For reasons of risk mitigation, multiple parallel bioreactors might be preferred. The process diagram is shown in Fig. 1. Dry air, pure O_2, or a mixture thereof is sparged at the bottom of the bioreactor through orifice spargers. The off-gas exits at the top and is a mixture of unconsumed feed gas, produced CO_2, and evaporated water. C-source is fed at a limiting rate and N-source (20 wt % aqueous ammonia) is fed according to its stoichiometric requirements. With assumptions of high affinity of the microbes for the carbon source (low K_s values), low setpoint concentration in the bioreactor for N-source, and ideal mixing, this leads to negligible residual C-source and ammonia levels. Therefore, evaporation of C-source and ammonia are neglected. Broth cooling is performed using an external cooling loop [5].

Bioreactor performance was modelled via mass balances (Table S4) that account for flow rates (F), gas-liquid transfer (N_i), biological production rates (R_i), and mass of liquid (M_L). Details of the model and its assumptions are given in [5].

Before entering the bioreactor, the air and O_2 mixture is compressed to exceed the pressure at the bottom of the bioreactor. After fermentation, the broth containing microbial cells is concentrated to 20% solids by centrifugation, where 2% of cells are assumed to be lost in the supernatant. From this point on, the downstream process is identical for each C-source. The concentrated cell suspension undergoes evaporation to reach a solids concentration of 35%. The produced paste is finally dried in a spray dryer, and the SCP product is obtained with a solids concentration of 90% [12–14]. We assume no significant product loss during the evaporation and drying. So, according to the 2% biomass loss during centrifugation, 98% of the biomass is recovered. Liquid from centrifugation is sent to wastewater treatment (WWT). Contrarily, WWT was assumed unnecessary for the remaining residual water streams (condensate from evaporation and drying steps). Actual downstream processing may be done differently than in our simplified design, in which the type of microbe and SCP application are not considered, and no refining of dried SCP is pursued. Thus, our analysis is relevant for feed applications of SCP rather than for food applications.

2.3. Economic model and optimization approach

The economic feasibility of the SCP production processes was assessed by calculating the minimum selling price (MSP) of SCP using the NREL calculation method [15] for which the key economic parameters are given in Table S7. As economic lifetime of the plant, 15 rather than 30 years was taken, because SCP is not an established commodity product.

To identify the most cost-effective bioreactor operating conditions per C-source, the MSP of SCP was minimized. This was an optimization problem with 16 variables, 12 constraints and MSP as objective. There were therefore 4 degrees of freedom. The key operational variables were dilution rate (D), bottom pressure (p_{bot}), superficial gas velocity (v_{sG}), and inlet O_2 mole fraction ($y_{O2,in}$) of the gas phase, each within a range that was bounded by physiologically and operationally relevant limits (see Table 1).

Besides this, practical constraints were included for many dependent variables, such as $C_x = 0$ to 0.15 kg_x/kg for the biomass concentration in the bioreactor and $C_{S,feed} = 0$ to 1 kg_s/kg for the C-source in the feed flow [5]. The optimization was carried out using the sequential quadratic programming (SQP) algorithm implemented in MATLAB's *fmincon* function.

To do so, capital expenditures (CAPEX) and operational expenditures (OPEX) were estimated using established methods given in Supplementary file 1. Used prices of raw materials and utilities are provided in Table S6. Utility costs were calculated for gas compression, bioreactor cooling, centrifugation, evaporation, and drying as indicated in Supplementary file 1. Purchase costs of the main equipment were calculated from the size of the equipment using equipment-dependent equations,

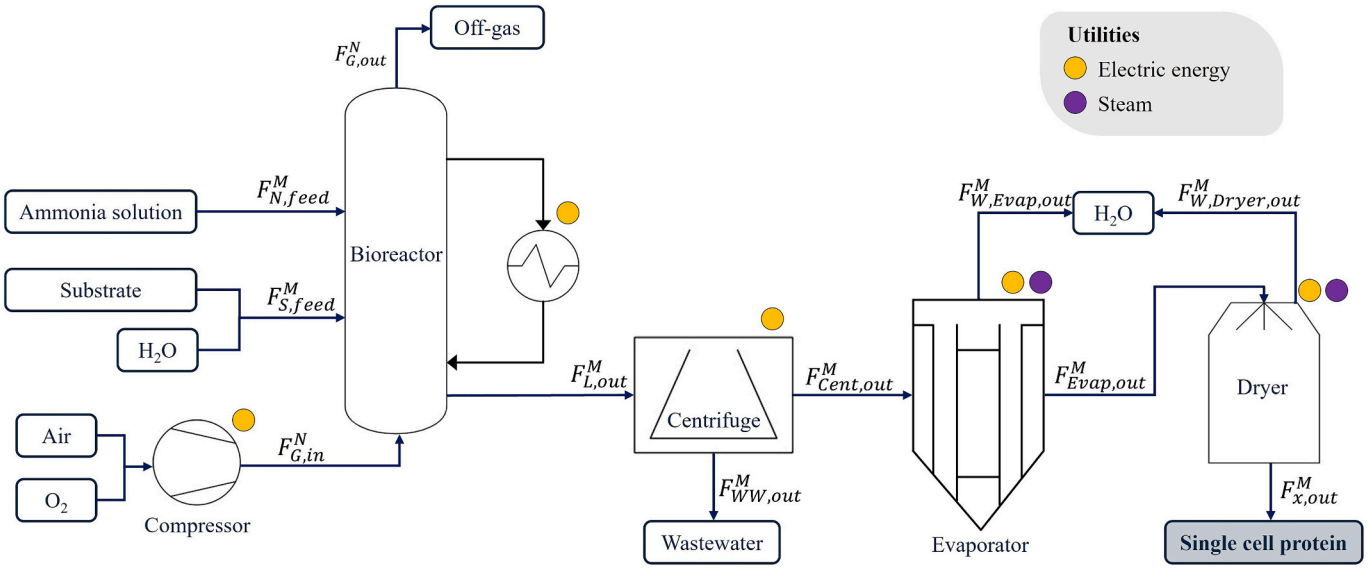

Fig. 1. Configuration of the simulated SCP production process.

Table 1
Ranges of the key operational variables used for optimization.

Input variable	Range	Comments
Dilution rate, h^{-1}	0.1–0.3	Feasible range according to μ^{max} and preliminary analyses.
Bottom pressure, bar (absolute)	1.2–4.0	The minimum prevents contamination and the maximum is due to range of the available economic model for the bioreactor.
Superficial gas velocity, m/s	0.04–0.30	Minimum at onset of the heterogenous bubbling regime and maximum at the validity limit of the used mass transfer model.
O_2 mol fraction in the gas feed	0.21–1.00	Intermediate compositions are combinations of air and pure O_2.

taking into account the equipment size range for the used equations (Table S.8). In the case of the bioreactor pricing, the operating pressure was additionally considered. The equipment purchase costs were multiplied by a factor of 1.2 to account for minor equipment, such as pumps that were not designed [16]. The additional multiplication factors for calculating CAPEX that lead to a very low Lang factor of 3.5 for designing plants for large-scale commodities [15] were replaced by an Lang factor of 7, which is more in line with SCP production economics [17].

2.4. Theoretical biomass yield calculation

Base-case MSP values were calculated using high experimental biomass yield values reported for different microbes. However, for comparison, a genome-scale metabolic model (GSM) of *Saccharomyces cerevisiae* (iMM904-GM) was employed to estimate theoretical biomass yields on different C-sources. The model was chosen for its moderate size and interpretability compared to more recent yeast GSMs, while still providing comprehensive metabolic coverage. Simulations were performed assuming zero maintenance energy to enable a direct comparison among C-sources. For C-sources that do not naturally support yeast growth, only O_2-insensitive natural or experimentally validated pathways were considered. The yield calculations were carried out in MATLAB R2018a using the COBRA Toolbox v3.0 [18]. Detailed model setup, pathway selection, and parameter information are provided in Supplementary file 1.

2.5. Sensitivity analysis

The sensitivity of the MSP was studied using different model inputs for prices, maximum yields, maximum dilution rate, k_La., and production scale. The MSP minimization procedure was re-run for each case, such that different values were found for model variables in each case.

3. Results and discussion

3.1. Reaction stoichiometry

The different reported experimental yields of biomass on C-source lead to large stoichiometric differences for consumed O_2 and produced CO_2 and H_2O, as shown in Table 2. Particularly, the different quantities of O_2 and CO_2 will have an impact on the process designs shown later. For the used biomass formula ($CH_{1.8}N_{0.2}O_{0.5}$), the degree of reduction per carbon atom is $\gamma/n_C = 4.2$ mol_e/mol. C-sources with almost similar γ/n_C values (glucose, glycerol, acetic acid, and lactic acid) show modest stoichiometric coefficients for both O_2 and CO_2, because their conversion into biomass needs overall relatively few oxidation and reduction steps. C-sources that are significantly more reduced than biomass, hence with a high value of γ/n_C (methanol and ethanol), also show modest O_2 consumption per amount of biomass but produce less CO_2. On the other hand, relatively oxidized C-sources (formic acid, glycolic acid, and oxalic acid) show much more CO_2 production than O_2 consumption. Besides, they show high O_2 consumption levels because of poor Gibbs free energy release during their catabolic conversion and the high

Table 2
Molar stoichiometric coefficients for production of 1 mol dry biomass (X, assumed to be represented by $CH_{1.8}N_{0.2}O_{0.5}$) according to the experimental yields of biomass on C-source (S) of Table S1 and element balances. The degree of reduction per carbon atom in the C-source (γ/n_C) is also shown.

C-source	S	O_2	NH_3	X	CO_2	H_2O	γ/n_C
Glucose	−0.249	−0.441	−0.200	1	0.491	0.891	4
Glycerol	−0.461	−0.564	−0.200	1	0.383	1.244	4.67
Methanol	−1.372	−1.009	−0.200	1	0.372	2.145	6
Ethanol	−0.660	−0.930	−0.200	1	0.320	1.380	6
Acetic acid	−1.051	−1.053	−0.200	1	1.103	1.503	4
Lactic acid	−0.667	−0.950	−0.200	1	1.000	1.400	4
Formic acid	−5.449	−1.674	−0.200	1	4.449	4.849	2
Oxalic acid	−5.363	−1.632	−0.200	1	9.726	4.763	1
Glycolic acid	−2.218	−2.277	−0.200	1	3.436	3.836	3

amount of Gibbs free energy needed for their anabolic conversion into biomass (Table S3).

3.2. Bioreactor performance

To assess the economic feasibility of SCP production from different C-sources, each bioreactor was evaluated under its own optimized conditions. The values of the key operational variables obtained after optimization to the lowest MSP hardly varied across C-sources. For each C-source, the optimized superficial gas velocity was $v_{sG} = 0.30$ m/s and the bottom pressure was $p_{bot} = 4$ bar, both at the upper boundary of their range, thus maximizing O_2 transfer and therefore SCP productivity. This leads to smaller bioreactors, and hence costs reductions that compensate extra bioreactor purchase costs due to the higher pressure and larger air compression costs. However, the optimization leads to use of air without O_2 addition for each C-source, since pure O_2 purchase costs were too high. (Later, sensitivity analysis will show that a lower O_2 price can lead to a very different optimization outcome.) The optimized dilution rate D (see Table 3) was at its upper boundary (0.30 h^{-1}) for glucose and lactic acid, but was lower for other C-sources. A higher dilution rate leads to a lower biomass concentration, which increases downstream costs, but also leads to higher specific growth rates, hence biomass yields closer to the maximum biomass yield, and lower C-source costs.

According to the mass transfer model used, $v_{sG} = 0.30$ m/s leads to $k_La = 0.171$ s^{-1} and gas holdup $\varepsilon_G = 0.26$ for each C-source. The resulting specific O_2 transfer rate falls within the range 0.30–0.35 mol/(h·kg_L) for most C-sources (see Table 4). For formic, oxalic, and glycolic acid it is lower, in the range of 0.20–0.24 mol/(h·kg_L), because excessive CO_2 production decreases the mole fraction of O_2 in the gas phase and thereby the driving force for O_2 transfer. Despite these relatively small differences, plus relatively small differences in only one key operational variable (Table 3), large differences occur in key reactor performance metrics such as biomass concentration, productivity, and extent of O_2 utilization (Table 4). Glucose results in the highest biomass concentration (59 g_x/kg_L) and volume-specific productivity (17.7 g_x kg_L^{-1} h^{-1}), both as consequences of efficient microbial growth and low O_2 demand, ultimately leading to a relatively small bioreactor (124 m^3). In contrast, formic, oxalic and glycolic acid exhibit low biomass concentrations (11–16 g_x/kg_L) and low productivities (2.3–3.4 g_x kg_L^{-1} h^{-1}), reflecting higher C-source and O_2 requirements for cell synthesis, and leading to 640–940 m^3 bioreactor volume, close to the maximum reported size [19]. The C-source concentrations needed in the feed vary even more, because they depend on achievable biomass concentration (determined by O_2 transfer rate) and biomass yield on C-source. For ethanol, 55 g/kg_{feed} suffices. Oxalic acid would need to be at 222 g/kg_{feed}, which is beyond its aqueous solubility of 120 g/kg at 30 °C [20]. So, oxalic acid might have to be fed as slurry. The case of avoiding slurry feeding was also considered by adding to the model a constraint that limited the oxalic acid concentration in the C-source feed stream to its solubility. This almost 50% higher dilution increased the MSP from 16.19 to 16.51 $/kg, because it almost doubles the amount of water needed and wastewater produced, and leads to a larger bioreactor and centrifuge.

Table 3
Optimal conditions for the dilution rate.

C-source	D (h^{-1})
Glucose	0.30
Glycerol	0.26
Methanol	0.17
Ethanol	0.19
Acetic acid	0.19
Lactic acid	0.30
Formic acid	0.21
Oxalic acid	0.22
Glycolic acid	0.21

The dissolved CO_2 concentration ranges from 2 mmol/kg for the most reduced C-sources (methanol, ethanol) to 19 mmol/kg for the most oxidized C-source (oxalic acid), as shown in Table 4. As discussed before [5] experiments are needed to assess if inhibition occurs at such concentrations. Similarly, potential O_2 toxicity at high pressures should be experimentally evaluated.

Heat generation is roughly proportional to O_2 consumption, ranging from 3.7 MW for glucose to 18 MW for glycolic acid. As mentioned before [5], removing such amounts of heat poses significant technical challenges and requires a carefully designed heat-exchange system to ensure effective temperature control. Feasibility needs a deeper study.

Biomass yields on C-source were 96–98% of the used literature values, which, for simplicity, had been assumed as maximum biomass yields. In general, the optimization selects dilution rates at which maintenance becomes negligible, without diluting the biomass concentration too much. C-source utilization was close to 100%, made possible by the choice of $K_s = 1$ mmol/L, which leads to residual concentrations of C-source of the same order of magnitude. Due to these low concentrations, C-source toxicity to the cells [21] can be prevented if liquid mixing is adequate, maybe in combination with multiple feed inlet points. Calculation of the vapor pressure of the most volatile C-source (methanol) showed that the assumption of negligible loss to the vapor phase is valid (Supplementary file 1). The low residual C-source concentrations after fermentation (~1 mmol/kg_L) might increase, for non-volatile C-sources, by a factor of about 5 in the dried SCP due to the evaporation and drying steps. This factor stems from the assumption of obtaining 20% solids after centrifugation. Depending on the SCP application, on C-source, and on the selected downstream operations, additional downstream steps need to be included to remove such C-source traces.

3.3. Economic performance of the overall SCP production

Equipment purchase costs are in the range of 2.4–7.0 M$ excluding an estimated 20% non-designed equipment (Fig. 2A). Upstream purchase costs (the bioreactor, seed train, compressor, and the bioreactor's cooling loop) are higher for C-sources that cause higher rates of O_2 consumption. Because of the fixed SCP production capacity, the stream size sent to centrifugation depends on the achieved biomass concentration in the broth, hence on C-source, leading to relatively low centrifuge purchase costs for glucose, glycerol, methanol and ethanol. Evaporator and dryers receive the same flow in each case. Therefore, their purchase costs are the same for each C-source. Overall, glucose has the lowest equipment purchase costs and glycolic acid the highest. These purchase costs lead to CAPEX values in the range of 20–60 M$.

These modest CAPEX values lead to a modest fixed part of the operational expenses (OPEX), as shown in the OPEX breakdown per kg SCP produced (Fig. 2B). OPEX is largely dominated by its variable part, in particular C-source costs. These are relatively low for glucose, glycerol, methanol, and ethanol, which combine low C-source prices with high productivity and biomass yield, resulting in C-source cost shares of only ~60% of OPEX. Acetic acid is lagging behind these four C-sources, and lactic acid occupies an intermediate position between acetic acid and the other carboxylic acids (formic, glycolic and oxalic acid). The latter three have very high C-source costs because they combine low biomass yields (as they are relatively oxidized) with high C-source prices. The costs in Fig. 2B include a fixed, small portion of ammonia costs (0.09 $/$kg_x$) as ammonia is almost completely consumed, and the produced biomass is assumed to have a fixed nitrogen content. Utility costs are in the range of 0.25–0.58 $/$kg_x$, including a relatively large proportion of air compression energy costs and bioreactor cooling costs for C-sources that need much O_2 (formic, oxalic, and glycolic acid), whereas these cost contributions are much lower for glucose. Downstream, most utility costs are due to energy for evaporation and drying, whereas centrifugation does not need much energy. Besides, the aqueous supernatant flow from centrifugation does not lead to large wastewater

Table 4
Key reactor performance indicators at optimized conditions for each C-source.

C-source	Bioreactor volume (m^3)	Specific productivity ($g_x \cdot h^{-1} \cdot kg_L^{-1}$)	Feed C-source concentration ($g_s \cdot kg_L^{-1}$)	Broth mass ($tonne_L$)	Biomass concentration ($g_x \cdot kg_L^{-1}$)	O_2 transfer ($mol \cdot kg_L^{-1} \cdot h^{-1}$)	O_2 utilization (%)	Heat production (MW)	Biomass yield on C-source ($g_x \cdot g_s^{-1}$)
Glucose	124	17.70	113	87	59.1	0.353	14.88%	3.7	0.532
Glycerol	160	13.68	95	113	51.8	0.345	16.05%	4.8	0.560
Methanol	314	6.99	80	221	41.0	0.312	19.21%	8.8	0.536
Ethanol	284	7.71	55	200	40.8	0.318	18.75%	7.2	0.776
Acetic acid	338	6.49	90	238	34.0	0.299	19.32%	7.5	0.375
Lactic acid	289	7.58	63	204	25.3	0.309	18.58%	7.0	0.399
Formic acid	647	3.39	155	456	16.3	0.239	21.74%	15.2	0.096
Oxalic acid	738	2.97	222	520	13.5	0.203	21.00%	14.2	0.050
Glycolic acid	937	2.34	75	660	11.1	0.223	24.10%	18.2	0.143

treatment costs. Therefore, utility costs only weakly depend on the achieved biomass concentration in the broth.

Overall, glucose emerges as the most favorable option, with the lowest OPEX, due to its combination of low C-source price, high biomass yield, and low O_2 demand. The MSP (Fig. 2C) follows the same trend as the OPEX, because CAPEX does not have a major influence. The MSP values of glucose, glycerol methanol, and ethanol fall in a narrow range, 2.40–2.59 $/kg$_x$, which is ~40% higher than the current fishmeal selling price of ~1.8 $/kg$_x$ [22]. Error margins have not been calculated, but sensitivity analysis (see later) suggests that the MSP differences between these four substrates are hardly significant. Acetic acid leads to a ~ 30% higher MSP (3.23 $/kg), whereas the MSP values calculated for lactic, formic, glycolic and oxalic acid are beyond 7 $/kg. At current raw material prices, the latter four C-sources are therefore economically unattractive for SCP production. Since the C-source cost is the dominant contributor to total production cost, it will be further examined in the sensitivity analysis.

3.4. Discussion on the impact of assumptions

3.4.1. Sensitivity to C-source price

The current market prices are based on agricultural feedstocks for glucose, ethanol, and lactic acid, on petrochemical feedstocks for methanol, formic acid, acetic acid, and glycolic acid, and on both for glycerol and oxalic acid. These prices are very time- and location sensitive. The used prices of the economically attractive C-sources are all from 2025 for Western-Europe, and from the same information source [23]. The prices from the same reference for the USA and China were on average 5 and 33% lower. Individual prices can differ much more. Therefore, we analyzed the sensitivity of the MSP to the C-source prices in the range of 20–180% of the base-case prices.

As the model shows, the MSP is mostly determined by the C-source price. In fact, a predictor is simply the ratio of this price and the biomass yield. The nearly linear behavior of the MSP with C-source price (see Fig. 3) is explained by this. To obtain an MSP of 2 $/kg, the C-source prices (in $/kg$_s$) needed are 0.24 for acetic acid, 0.35 for methanol, 0.47 for glucose and glycerol, and 0.54 for ethanol. This would require a very optimistic C-source price reduction of 63% for acetic acid, but for the others such a reduction would be more feasible, in the range of 31–45%. C-sources with high feedstock contribution to OPEX in Fig. 2B (lactic, glycolic, oxalic, and formic acid) exhibit an even higher sensitivity (Fig. 3B). The slopes differ in Fig. 3 because the biomass yields are different. Changing C-source prices by the same percentage does not alter the MSP ranking.

Since re-optimization of operating conditions was used for sensitivity analysis, the operating conditions shift with C-source price, but these shifts are not shown nor discussed here.

3.4.2. Influence of maximum biomass yield

As C-source costs have a significant impact on the MSP, the choice of the used maximum yield of biomass on C-source was also checked. A 30% decrease in the maximum yield on ethanol, for example, increases the required amount of ethanol by about 30% but leads to a more than proportional (35%) increase in MSP, because the productivity decreases, leading to higher compression, bioreactor, and centrifugation costs per amount of SCP. Because of the importance of the maximum biomass yields, we also used calculations to obtain these yields, using a genome-scale model of *S. cerevisiae* (see Supplementary file 1). This is a typical industrial microbe, although its genome may be not representative for other yeasts and certainly not for prokaryotes. Most calculated yields were slightly lower than experimental yields used in this paper, suggesting that the experimental strains used a more efficient metabolism than *S. cerevisiae*, which has a P/O ratio of merely 1. Consequently, as shown in Fig. 4, using calculated rather than experimental yields led to higher MSP values in most cases. This was not the case for methanol and glycolic acid, for which calculated yields were higher than experimental yields, suggesting that there is still room for improvement of the experimental yield for glycolic acid and methanol according to the genome-scale model. Although the MSP for glycolic acid was calculated to decrease by 38% if the yield would be improved to the calculated value, the MSP will still be relatively high. Contrarily, methanol would become the C-source with the lowest MSP in case the theoretical yield is achieved in practice (see Fig. 4).

3.4.3. Cost of pure O_2

One may imagine a future scenario in which pure O_2 would be almost freely available because, in the proximity of the SCP production plant, a fermentation C-source might be produced electrochemically and the co-produced O_2 would otherwise be emitted into the atmosphere. We evaluated the sensitivity of the MSP to the O_2 price of that scenario. Decreasing the O_2 price (0.16 $/kg) by 90% leads to switching to the use of pure O_2 for all C-sources. Fig. 4 shows that the MSP decreases by 0.08–0.10 $/kg$_x$ for C-sources that have low O_2 requirements (glucose, glycerol), by 0.15–0.19 $/kg$_x$ for C-sources that demand intermediate amounts of O_2 (methanol, ethanol, acetic acid, lactic acid) and by 0.30–0.43 $/kg$_x$ in the case with a high O_2 demand (formic, oxalic and glycolic acid). For this scenario, the lowest MSP values were 2.31 $/kg$_x$ for glucose and 2.35 $/kg for methanol.

The origin of the switch to pure O_2 in case of a low pure O_2 price is that the main disadvantage of pure O_2 (its costs) is more than compensated by its advantages: the equilibrium solubility of O_2 becomes almost fivefold higher, leading to a proportionally faster O_2 mass transfer, and hence to a higher volume-specific productivity, and to a smaller bioreactor. About five times less gas flow is needed, which saves on gas compression costs. Besides, a lower gas flow rate slightly decreases the gas hold-up in the bioreactor, contributing to a higher broth content and hence a smaller bioreactor. Overall, the bioreactor volume

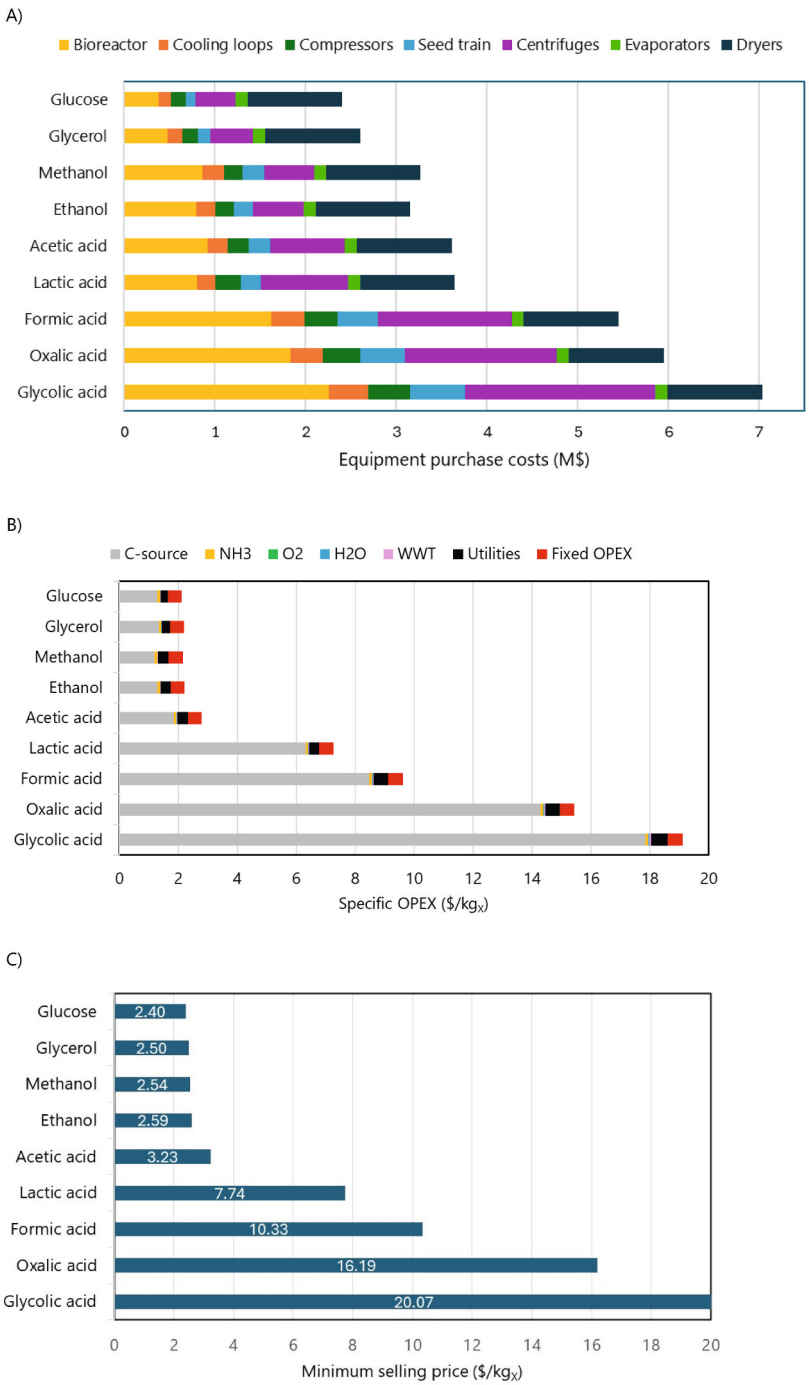

Fig. 2. Techno-economic performance indicators for the nine evaluated C-sources under optimal operating conditions. A) Purchased equipment costs; B) Specific OPEX; C) MSP.

decreased by at least 60% and the biomass concentrations more than doubled for all C-sources. At about 30% of the base-case O_2 price, there is a breakeven between using air or pure O_2. Obviously, acquiring cheap, pure O_2 for use in SCP production is an important strategy. However, attention points are potential inhibition by O_2 and especially CO_2 because of their higher partial pressures, the higher cooling demand, and the higher risk of concentration gradients formation in the bioreactor at the lower gas flow rate.

In these simulations, in the absence of biological data for inhibition by CO_2, we did not find optimized scenarios that used mixtures of air and pure O_2. Local optima were found that used either only air or only pure O_2, and either of them was the global optimum.

3.4.4. *Higher dilution rates*

One of the constraints of the MSP minimization was the maximum dilution rate of $D = 0.30\ h^{-1}$, which is feasible for each C-source according to maximum growth rates that were calculated using thermodynamic correlations (Table S3). For several C-sources, much higher D-values are feasible according to published μ^{max} values [24,25]. When the constraint was relaxed to a maximum of $D = 0.40\ h^{-1}$ during MSP minimization, only lactic acid showed an increased D value ($0.31\ h^{-1}$) with virtually no impact on MSP. The slightly increased biomass yield (relatively less C-source needed for maintenance) was almost completely offset by higher centrifugation and wastewater treatment costs (more dilute broth at higher D). On the other hand, MSP values increased only

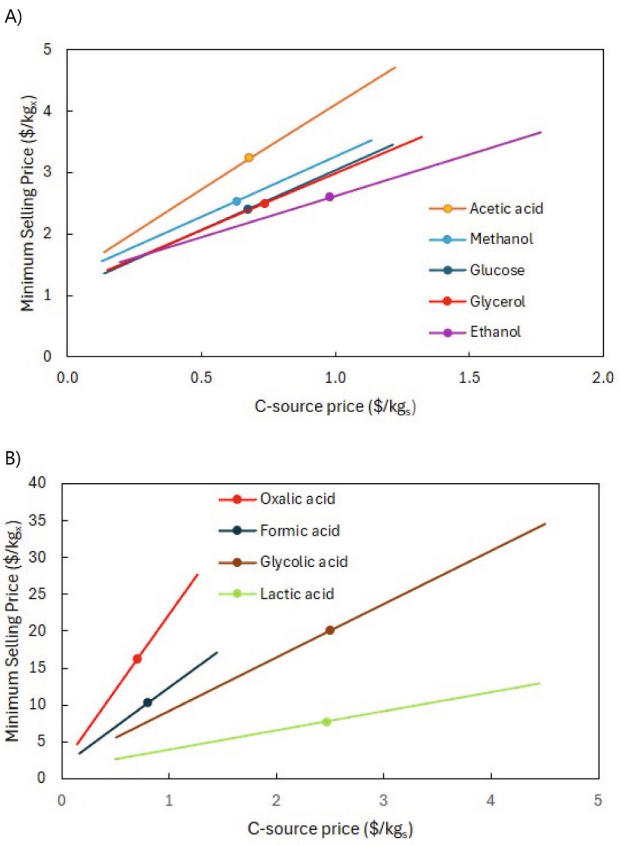

Fig. 3. Sensitivity of the minimum selling price (MSP) to deviations (±80%) from the base-case C-source price, which is indicated by the markers. A) Base-case MSP below 4 $/kg$_X$. B) Base-case MSP above 7 $/kg$_X$.

slightly when imposing $D = 0.20\ h^{-1}$ as maximum. Thus, focusing at obtaining μ^{max} values beyond 0.30 h^{-1} is not a promising strategy.

3.4.5. Utility prices

Utility costs are a minor contributor to OPEX (see Fig. 2C), with electricity costs being the most important utility costs, mostly for the compressor (Fig. S4). A 50% lower electricity price decreases the MSP of glucose, glycerol, methanol, ethanol, and acetic acid by 3–5% (0.07–0.12 $/kg$_x$) and the MSP of the other acids by 1–2%. Thus, electricity costs are a significant but not dominating cost driver. Utility costs may have a larger, indirect effect on the prices of the C-sources, but that effect is out of scope here.

3.4.6. k_La

The model used for predicting the mass transfer coefficient k_La is valid for oxygenating pure water [5]. Solutes in fermentation broth may significantly change k_La, in particular by decreasing bubble size and hence increasing the specific gas-liquid interfacial area a. For example, 1 wt% ethanol can double k_La [26]. Even though the concentrations of solutes in broth are much lower in our predictions, and coalescence inhibition properties vary per type of feedstock, we evaluated the effect of doubling k_La. The effect on MSP was weaker than the effect of decreasing the O_2 price by 90%. The MSP decreases by 0.09–0.10 $/kg$_x$ for C-sources that do not need much O_2 (glucose, glycerol), by 0.14–0.19 $/kg$_x$ for C-sources that demand intermediate amounts of O_2 (methanol, ethanol, acetic acid, lactic acid) and by 0.30–0.43 $/kg$_x$ in the case with a high O_2 demand (formic, oxalic and glycolic acid). The lowest MSP was 2.32 $/kg$_x$, for glucose. These are significant effects, showing the value of precise k_La data.

3.4.7. Production scale

Choosing 12 ktonne/year SCP production allowed for each C-source the use of a single bioreactor within the size range of the available bioreactor cost model. Splitting the base-case throughput of 12 ktonne/year SCP between two bioreactors that produce 6 ktonne/year may be needed for technical reasons or for risk mitigation. Reoptimization led for each C-source to an increase in MSP of about 0.5 $/kg$_x$. Optimized conditions include a slightly smaller total bioreactor volume (summed for the two parallel bioreactors). This smaller volume needs a higher volume-specific O_2 transfer (more air and a higher top pressure) to achieve the desired throughput. In the base case, a single equipment unit is also needed for downstream operations, except for drying which needs two parallel drying units because of their relatively low capacity, and centrifugation. Centrifugation needs multiple units for the acids (two for acetic acid and lactic; three for formic and oxalic, and four for glycolic), in line with higher flow rates to centrifugation because of lower biomass concentrations in the bioreactor outflow. Gradual increases in

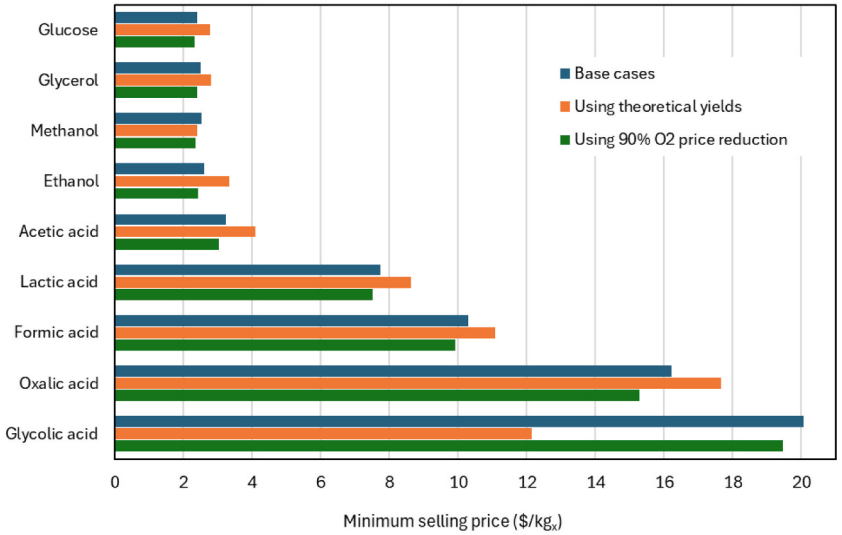

Fig. 4. Techno-economic performance of the nine evaluated carbon sources, represented by the minimum selling price (MSP) for the base cases (Section 3.3), for the base cases but using biomass yields on C-source according to the genome-scale model (Section 3.4.2), and for the base cases but with the pure O_2 price reduced by 90% (Section 3.4.3). Operation conditions were individually optimized.

production scale will gradually lower the CAPEX per kg SCP produced because larger equipment has lower costs per volume. This continues until some maximum equipment size is reached, requiring splitting over multiple smaller pieces of parallel equipment per type, which results in a step-up in CAPEX. Overall, CAPEX roughly decreases with increasing scale, with discontinuities that depend on C-source and maximum capacity per equipment type. Doubling the production scale to 24 ktonne/year SCP still led to a single bioreactor, except for formic, oxalic and glycolic acid. The MSP for the other six C-sources decreased by 0.23–0.25 $/kg$_x$, which shows the benefit of maximizing the bioreactor size. At 60 ktonne/year SCP production, only glucose still required merely one bioreactor below the maximum volume of the used range (1000 m^3), with MSP dropping to 2.02 $/kg$_x$ as compared to 2.40 $/kg$_x$ in the base case.

3.4.8. C-sources considered

This study evaluates undissociated carboxylic acids (e.g. acetic acid) as C-source rather than the corresponding carboxylate salts (e.g. sodium acetate). The used bioreactor model [5] assumes substrate-limited chemostat operation, such that the bioreactor and its outflow contain a low residual concentration of unconverted C-source. If, for example sodium acetate rather than acetic acid is used as the C-source for SCP production, consumption of this sodium acetate leads to formation of sodium hydroxide, such that a stoichiometric amount of acid titrant (e.g. H_2SO_4) is needed for pH control. In mass terms, more inorganic salt (Na_2SO_4 in this example) than SCP would be produced, also leading to osmotic values in the bioreactor that could inhibit microbial growth. In a next process step, the formed salt needs to be removed from the SCP and needs to be disposed or re-used in some way at significant cost [27]. Thus, designing the use of a carboxylate salt as C-source would add both complexity and costs. In contrast, when feeding undissociated carboxylic acid to a carbon-limited culture, thus at very low residual concentration, simultaneous consumption of this carboxylic acid prevents that pH drift occurs.

Also, gaseous C-sources (CH_4, CO, and the combination $CO_2 + H_2$) have not been discussed, even though they are gaining a lot of interest [12]. Aerobic conversion of gaseous C-sources leads to flammability and explosion risks that significantly increase CAPEX and operational complexity [28,29]. Moreover, the partial pressure of a gaseous C-source and its percentage utilization need to be optimized, which adds two degrees of freedom to the bioreactor design. For gaseous C-sources, the design becomes sensitive to the value used for the substrate affinity constant K_s, which is uncertain. Besides, heat production for gaseous C-sources is much larger than for non-gaseous C-sources because of much larger entropy losses. Future studies should try to mitigate these design issues.

3.4.9. Maintenance coefficients, maximum uptake rates, and C-source affinity

The maintenance coefficients (m_s) and maximum uptake rates (q_s^{max}) were estimated using literature correlations rather than experimental data (Section 2.1). Such correlations provide merely order-of-magnitude values. Lower m_s values lead to lower C-source costs for maintenance. When changing m_s from −50% to +50% of its base-case value, the MSP values were, dependent on C-source, 1.2 to 4.6% lower for the −50% case as compared to the +50% case. For the −50% cases, it is less important to operate at high growth rates because the maintenance penalty is less significant. This led to dilution rates that were up to 43% lower than for the +50% case. The liquid feeds and outflows become significantly smaller and more concentrated, leading to cost advantages in downstream processing, which did not significantly change overall costs. Thus, experimental determination of the actual m_s values is important for process design, but the ranking of C-sources will hardly be affected by values different from what we used.

When changing q_s^{max} from −50% to +50% of its base-case value, the MSP values and operational conditions were generally hardly affected. The residual C-source concentration changed significantly, but not to the extent that C-source loss with liquid outflow or with off-gas became important.

In the base-case model, a guess value of $K_s = 1$ mmol/L has been used, which is highly uncertain. Calculations using $K_s = 0.1$ mmol/L led to negligible decreases in MSP, because the residual unconsumed C-source concentration decreased even further. Using $K_s = 10$ mmol/L led to stronger, opposite effects, with MSP values that increased by 0.1 to 0.8% relative to their base-case values, due to higher residual C-source concentrations. Using $K_s = 100$ mmol/L led to MSP values that increased by 0.6 to 3.2% relative to their base-case values. These trends indicate that obtaining strains with a low K_s value is important.

3.4.10. Microbe

The choice of the microbe is critical, not merely for achieving the biomass yields discussed before. The SCP processes designed here assume that suitable microbes can be found for commercial production according to the designed processes. However, elemental formula and kinetic parameters differ per microbial strain, and many other microbial factors such as the resulting broth viscosity will influence its processing. Moreover, food and feed markets will have numerous application-related requirements on the produced SCP such as the crude protein content, average amino acid composition of the protein fraction, digestibility, palatability, absence of anti-nutritional factors, etc. [30,31]. These factors need to be considered in a more detailed design on SCP production from a preferred C-source.

Downstream processing might also vary with microbe type. For example, bacteria are generally smaller and harder to dewater than yeast, and microbe-specific optimization is a necessary next step before final C-source selection. The current analysis assumes fixed downstream operation conditions, though. Doubling the equipment and utility costs for all downstream processing steps increased the MSP by 0.31–0.32 $/kg$_x$ for most C-sources, but by 0.38–0.51 $/kg$_x$ for the less favorable C-sources (lactic, formic, oxalic, and glycolic acid). These would be significant additional costs.

4. Conclusions

At current market prices, glucose, glycerol, methanol, and ethanol are the most promising C-sources for large scale SCP production. They combine low C-source price, high biomass yield, and high volumetric productivity with moderate O_2 demand, overall leading to an MSP of about 2.5 $/ kg$_x$. Acetic acid leads to a somewhat higher MSP, whereas lactic, formic, glycolic and oxalic acids are currently much less competitive due to low yield, low productivity, and high C-source price, leading to MSP values of 7–20 $/kg$_x$.

The economic performance of SCP production is primarily dictated by C-source price and biomass yield on C-source, since raw material costs contribute 60% or more to the plant operation costs. Utility costs and investment-related costs jointly contribute less than 40% to overall costs. Therefore, research focused on increasing biomass yields and lowering C-source prices, possibly through improved technologies and process integration, will lead to enhanced economic feasibility of SCP production. In addition, switching from air to pure O_2 will be favorable in the case O_2 can be purchased at about 30% of its current price.

Future work should expand this techno-economic framework to include environmental assessment (e.g., carbon footprint, avoided nitrogen emissions for conventional protein value chains, energy demand) in scenarios with industrial production of C-sources from biogenic CO_2, while harnessing the low carbon footprints of renewable energy.

CRediT authorship contribution statement

Eduardo Almeida Benalcázar: Writing – original draft, Methodology, Investigation, Conceptualization. **Rodoula Ktori:** Writing – original draft, Methodology, Investigation. **Peter J.T. Verheijen:** Writing –

review & editing, Methodology, Investigation. **Liang Wu:** Writing – original draft, Methodology, Investigation. **Wouter A. van Winden:** Writing – review & editing. **Mickel L.A. Jansen:** Writing – review & editing. **Henk Noorman:** Writing – review & editing. **Adrie J.J. Straathof:** Writing – original draft, Supervision, Methodology, Investigation, Conceptualization.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cej.2026.180714.

Data availability

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

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