Valorising fermentation effluent rich in short-chain fatty acids and sugars for biohydrogen via photofermentation by Rhodobacter sphaeroides KKU-PS1

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Abstract. Growing fermentative chemical production will increase effluents from industrial fermentations containing short-chain fatty acids and residual sugars, which are exploitable for biohydrogen through photofermentation. Previous studies have concentrated on single substrates and photofermentation study using fermentation effluent from bio-succinate production containing residual sugars and short-chain organic acids has yet to be reported to the best of authors’ knowledge. Rhodobacter sphaeroides KKU-PS1 grown on succinate was used for hydrogen production from medium containing mixture of substrates mimicking final effluent from bio-based succinate production. Prior to that, hydrogen producibility test with succinate-only medium was carried out. Photofermentation from succinate by this strain yielded 1217 ml H2/l of maximum cumulative hydrogen with maximum hydrogen rate of 6.7 ml H2/l/h, comparable to malate which was previously reported as best single substrate for the strain. Hydrogen production profiles using mixed substrates was well-fitted by modified Gompertz model with maximum cumulative hydrogen and maximum hydrogen production rate of 1005 ml H2/l and 4.1 ml H2/l/h, respectively. Only glucose, xylose and succinate followed modified Gompertz model for substrate consumption. Instantaneous succinate consumption compared to extended lag time of 100h for consumption of both sugars indicated higher affinity towards short-chain fatty acid utilization during initial growth phase. Xylose showed highest overall substrate consumption signifying its importance for hydrogen generation, which continued after stationary growth phase started reaching a total of 91.9% consumption. Significant remaining substrate levels other than xylose suggested that the process was not inhibited by limited substrates. The study highlighted potential of fermentation effluents containing mixed substrates for biohydrogen, with further optimization needed.

1. Introduction
Growing fermentation industries particularly involving platform chemicals such as succinic acid could result in the increase of fermentation wastewaters rich in short-chain fatty acids as can be seen in alcohol processing industries [1,2]. Effluents from industrial fermentations particularly from the
downstream process of succinate production commonly contain unfermented feedstocks, unrecovered products and by-products such as short-chain fatty acids [3]. These effluents have immense potentials for hydrogen production through photofermentation using photosynthetic bacteria known as purple non-sulfur bacteria (PNSB) especially Rhodobacter sphaeroides which previously achieved high theoretical conversion efficiency from various substrates especially organic acids [4,5]. Previous studies have mostly been concentrating on single substrates [2,5–8]. Previous works using R. sphaeroides KKU-PS1 strain which was employed in this study, also used single substrates particularly malate [9,10]. Recently, photofermentation using alcohol distillery effluent containing sugars and volatile fatty acids (VFA) was studied yielding 1.2 l H2/l culture of hydrogen gas, revealing potentials of utilizing fermentation effluent for photofermentation [2]. However, to authors’ knowledge, photofermentative hydrogen production using effluents from bio-based fermentative succinate production or other similar effluents containing mixture of sugars and succinate has yet to be reported.

Therefore, in this study photofermentative hydrogen producibility and growth of R. sphaeroides KKU-PS1 strain using mixed carbon sources based on final effluent from fermentative bio-succinate production, were investigated along with kinetics associated with the process. Prior to that, hydrogen producibility from succinate, among major carbon sources of which the effluent comprised of, was confirmed before proceeding with the mixed substrates.

2. Materials and methods

2.1. Microorganism and media

Rhodobacter sphaeroides KKU-PS1 was obtained from Professor Alissara Reungsang from KhonKaen University, Thailand [9]. Growth medium was modified from RCVB medium, comprising of (all in g/l): KH2PO4 0.4, MgSO4.7H2O 0.4, NaCl 0.4, CaCl2 0.05, FeSO4 in Fe-EDTA complex form 0.001, and 1 mL of trace elements, and was added with 15 mM succinic acid, 4 mM sodium glutamate C4H8NNaO4H2O), and 1 g/l yeast extract. Hydrogen production medium (HPM) comprised of (in g/l): K2HPO4 2.8, KH2PO4 3.9, MgSO4.7H2O 0.2, CaCl2 0.075, Na2MoO4 0.02, FeSO4 in Fe-EDTA complex form 0.002, and 1 ml of trace elements [6].

2.2. Hydrogen producibility with succinate

Succinate and sodium glutamate was added to HPM at 15 mM and 3 mM, respectively, which was similar to C/N ratio used previously with malate as sole carbon source [9]. pH was adjusted to pH 7.0 by NaOH solution and then autoclaved. Sterile succinate-containing HPM was inoculated with 10% (v/v) of pre-cultured R. sphaeroides KKU-PS1 taken at exponential (log phase) growth phase, which was centrifuged and resuspended in HPM containing carbon sources at specified concentration above. Batch hydrogen production was carried out in triplicate, all of which incubated at temperature of 30±1 °C under illumination of light emitting diode (LED) light at 6700 lux and agitated at 150 rpm.

2.3. Biohydrogen production from mixed substrates mimicking bio-succinate crystallization effluent

This study used mixture of sugars and short-chain fatty acids based on composition of carbon sources in diluted crystallization effluents (data not shown) following bio-based succinate fermentation [3]. Glucose, xylose, succinate, acetate and formate at 6.6 mM, 10.5 mM, 10.4 mM, 7.7 mM, and 8.1 mM, respectively were added to HPM, which were lower than optimum concentration reported previously, respectively to avoid inhibition by high level of substrates [5,8,11]. 4mM of sodium glutamate was added as nitrogen source. pH was adjusted to pH 7.0 by NaOH solution and then autoclaved. Sterile HPM added with mixture of carbon sources specified above was inoculated with 10% (v/v) of pre-cultured R. sphaeroides KKU-PS1 taken at exponential (log phase) growth phase, which was centrifuged and resuspended in HPM containing carbon sources at specified concentration above. Batch hydrogen production was carried out in triplicate, all of which incubated at 30±1 °C under illumination of light emitting diode (LED) light at 6700 lux and agitated at 150 rpm.
2.4. Measurement and analysis
Gas produced by *R. sphaeroides* KKU-PS1 was collected using wetted syringe with needle by pressure-release method [6]. Cell concentrations were determined by a spectrophotometer at a wavelength of 660 nm. Light intensity was measured by using a luxmeter. Fermentation broth was analysed using high performance liquid chromatography (Agilent 1100, California, USA equipped with UV detector and Agilent 1200, California, USA equipped with RI detector) for fatty acids and sugars, respectively using ROA column and 0.0025 M H₂SO₄ as the mobile phase at a flow rate of 0.6 ml/min [12]. Biogas compositions were analysed by a gas chromatography using TCD detector at 200 °C, a packed column at 50 °C, and helium as carrier gas (Shimadzu GC-2014) [13].

2.5. Kinetic analysis
Representation of growth curve of *R. sphaeroides* KKU-PS1 was studied using modified logistic and Gompertz models, both of which used successfully in past studies [6,14]. Modified logistics model used was given by Equation 1 as used previously [15].

\[
X(t) = \frac{X_{\text{max}}}{1 + \exp[2 + \mu_{\text{max}}(\lambda - t)]}
\]

where X represents dry cell weight (g/l); X\(_{\text{max}}\) represents the maximum cell concentration (g/l); \(\mu_{\text{max}}\) represents the maximum specific growth rate (h\(^{-1}\)); \(\lambda\) is the lag time (h); and t is the culture time (h).

Modified Gompertz used in this study was based on modified version used previously as shown in Equation 2 [14,16], which is expressed as follows:

\[
\ln \frac{X}{X_0} = A \exp \left\{ - \exp \left[ \frac{\mu_{\text{max}} e}{A} (\lambda - t) + 1 \right] \right\}
\]

where \(X_0\) represents initial cell concentration (g/l); A is asymptote of the curve; \(e = 2.7182\); \(\lambda\) represents lag time (h); and t represents culture time (h). Modified Gompertz was employed for cumulative hydrogen production [17] as represented by Equation 3.

\[
H = H_{\text{max}} \exp \left\{ - \exp \left[ \frac{R_{\text{max,Hz}} e}{H_{\text{max}}} (\lambda - t) + 1 \right] \right\}
\]

where H is cumulative H₂ formation (ml H₂/l\(_{\text{culture}}\)); \(H_{\text{max}}\) is the maximum cumulative H₂ formation (ml H₂/l\(_{\text{culture}}\)); \(R_{\text{max,Hz}}\) is the maximum H₂ formation rate; \(\lambda\) represents lag time (h); and t is the culture time (h).

Substrate utilization was analysed by Modified Gompertz model as shown by Equation 4 [6]:

\[
S_0 - S = S_{\text{max}} \exp \left\{ - \exp \left[ \frac{R_{\text{max,S}} e}{S_{\text{max}}} (\lambda - t) + 1 \right] \right\}
\]

where S represents concentration of the substrate (mM); \(S_0\) represents initial concentration of substrate (mM); \(S_{\text{max}}\) is the maximum substrate concentration (mM); \(R_{\text{max,S}}\) represents maximum rate of substrate consumption (mM/h); \(\lambda\) refers to the lag time (h); and t represents culture time (h). Curve fitting and parameters estimation were accomplished by using Sigmaplot 11.0.

3. Results and discussion
3.1. Hydrogen producibility with succinate
Hydrogen production test run was conducted with succinate and sodium glutamate to compare hydrogen producibility of the strain using succinate with previous study using malate at similar concentration [9], results of which tabulated in Table 2. *R. sphaeroides* KKU-PS1 strain was able to achieve cumulative H₂ close to one in previous study using malate as shown in Table 2, which was among most preferred substrates for hydrogen production by several past studies [6,9]. Maximum hydrogen production rate (HPR) in this study at 6.7 ml H₂/l/h was also comparable with previous study. Since bio-based succinate production effluent contains high level of unrecovered succinate, potentially high yield of hydrogen can be achieved at high productivity comparable to the process with malate.

3.2. Biohydrogen production from mixed substrates mimicking bio-succinate crystallization effluent
Growth profile was fitted with logistic model due to multiple substrates used in this study since Monod model practicality with fermentation processes can be referred to growth limiting, carrier-mediated transport systems for single substrate [18]. Maximum biomass concentration, \(X_{\text{max}}\) of 1.09...
g/l obtained from logistic model shown in Table 1 matched the actual measured maximum biomass concentration value in experiment which was 1.09 g/l (data not shown). Good representation of experimental data by logistic model shown in Figure 1 suggests that growth R. sphaeroides KKU-PS1 in mixed substrates was not limited by substrate concentration as evident by high substrate concentration when growth decelerated to zero rate (stationary phase) approaching 200 h of fermentation in Figure 1. Instead, high cell concentration with maximum at 1.09 g/L in this study could be among limiting factors causing limited space for further cell growth and self-shading. In previous studies, growth curve of R. sphaeroides O.U.001 could not be fitted by Monod model, possibly due to non-substrate-limiting growth as shown by considerable level of remaining substrates at the start of stationary phase [19,20]. Modified Gompertz model was also used to compare with the logistic model. R^2 at 0.994 was higher than one obtained using logistic model, with smaller errors for both λ and µ_max respectively indicating better fit with Gompertz model. Interestingly µ_max predicted by both models shown in Table 1 were at almost same with not much difference in lag times. It is safe to say that µ_max and lag time for R. sphaeroides KKU-PS1 in mixed carbon source fell between 0.0236 h^{-1} to 0.0238 h^{-1} and 18.8 h to 20.5 h, respectively. In comparison, µ_max of R. sphaeroides KKU-PS1 was slightly lower than µ_max of R. capsulatus IR3 and R. sphaeroides obtained using Monod [21].

Table 1. Parameters by modified Gompertz and logistic models for hydrogen production and growth.

| Parameter | Gompertz H2 | Logistic Biomass | Gompertz Biomass |
|-----------|-------------|------------------|-----------------|
| H_max     | 1005 ± 28 ml H2/l | λ = 34.1 ± 7.2 h | ln(X/X_0)_max = 2.4822 ± 0.0306 |
| X_max     | 1.09 ± 0.02 g/l   | λ = 20.5 ± 9.6 h | λ = 18.8 ± 5.1 h |
| R_m       | 4.1 ± 0.3 ml H2/l/h | µ_max = 0.0236 ± 0.0025 h^{-1} | µ_max = 0.0238 ± 0.0022 h^{-1} |
| R^2       | 0.990          | 0.990            | 0.994           |

Figure 1. Growth, hydrogen production and substrate utilization profiles of R. sphaeroides KKU-PS1 in mixed substrates.
H<sub>max</sub> values for succinate and mixed carbon shown in Table 2 were close to measured cumulative hydrogen which were 1174 ml H<sub>2</sub>/l and 1029 ml H<sub>2</sub>/l (data not shown), respectively. Lag time, λ, obtained was different for the strain grown on succinate and mixed substrates, which were 20 h and 34 h, respectively, both of which are shorter compared to that obtained with malate in previous study [9]. Hydrogen production contributed by both growing cells and resting cells as demonstrated highest HPR near the end of exponential growth stage, and continued hydrogen production albeit relatively constant cell concentration afterwards, confirming previous observation [22]. The study also pointed out that under weak illumination, hydrogen is growth associated metabolite and as light intensity increased above 2500 lux, hydrogen production was contributed by combination of growth-associated and non-growth-associated metabolism with maximum HPR getting nearer towards stationary phase as light intensity increases [22].

**Table 2.** Parameters by modified Gompertz model for H2 production, substrate conversion efficiency (SCE) and H2 yield by *R. sphaeroides* KKU-PS1.

| Substrate        | H<sub>max</sub> (ml H<sub>2</sub>/l) | λ (h)       | R<sub>max</sub> (ml H<sub>2</sub>/l/h) | R<sup>2</sup> | SCE (%) | H<sub>2</sub> yield (mol H<sub>2</sub>/mol<sub>substrate</sub>) | References |
|------------------|-------------------------------|-------------|-------------------------------------|-------------|---------|---------------------------------------------------------------|------------|
| Malate 15 mM     | 1353 ± 34                     | 57.1 ± 5.6  | 6.8 ± 0.4                           | 0.990       | 64.1    | 3.85                                                          | [9]        |
| Succinate 15 mM  | 1217 ± 14                     | 23.2 ± 2.6  | 6.7 ± 0.2                           | 0.998       | 40.7    | 2.85                                                          | This study |
| Mixed carbon     | 1005 ± 28                     | 34.1 ± 7.2  | 4.1 ± 0.3                           | 0.990       | 17.4    | 1.31                                                          | This study |

Only glucose, xylose and succinate consumptions followed modified Gompertz model, with R<sup>2</sup> value of above 0.97 as shown Table 3. S<sub>0</sub> for each substrate were close to the measured initial substrate concentrations. Acetate and formate concentration curves (data not show) could not be fitted with the modified Gompertz model due to accumulation and no consumption, respectively. Succinate was readily consumed rapidly without lag time and reached plateau at about the same time as stationary phase began, indicating higher affinity towards utilizing succinate for growth, similar to malate as both can directly enter tricarboxylic acid cycle that provides energy for the bacteria [9]. Consumption rate of succinate was rapidly decreasing as fermentation proceeded especially approaching stationary phase of growth as shown by Figure 1. Total consumption of succinate throughout fermentation of 480 h was below 50% as shown in Table 3 although being preferred at initial stage of growth which could signify that the growth was not inhibited by limiting substrate per discussion above. Glucose and xylose profiles both showed lag time of about 100 h and started being significantly consumed during mid exponential stage of growth, indicating less preference for sugars for initial growth. Higher rate of consumption and total consumption shown by Table 3 indicated that xylose is preferred by *R. sphaeroides* than glucose throughout the fermentation. Significant xylose consumption together with relatively lesser glucose consumption was also reported with *Rhodobacter sphaeroides* 241EDD in a previous study implying higher preference towards xylose utilization compared to glucose by *R. sphaeroides* strains as observed in this study [23]. Acetate could be among metabolites from glucose and xylose consumption as its level surged to around 15 mM at 144 h before it dropped again at 216 h possibly being consumed for growth (data not shown). After 240 h of fermentation time or beginning of stationary phase, acetate level escalated rapidly possibly due to lower consumption of acetate during the stationary phase (data not shown).

Results of this study suggested that the growth and hydrogen production was not inhibited by limiting substrates, instead, possibly by insufficient space for growth and poor light penetration caused by relatively high biomass concentration compared to previous study [9]. Future practical applications should focus on light penetration in order to optimize the process. Overall, the cumulative hydrogen in this study was comparable with previous study using another fermentation effluent from alcohol
distillery plant, which has achieved 1.2 l H₂/l culture thus highlighting potential of this process for effluent from fermentative bio-succinate production [2].

| Table 3. Substrate consumption and parameters predicted by modified Gompertz model. |
|---------------------------------------------------------------|
| Substrate | S₀ (mmol/l) | λ (h) | Rₘₐₙₓ (mmol/l/h) | R² | Consumption (%) |
|-----------|-------------|-------|------------------|----|-----------------|
| Glucose   | 7.81 ± 0.11 | 109.7 ± 25.6 | 0.0134 ± 0.0027 | 0.9817 | 34.5 |
| Xylose    | 8.08 ± 0.21 | 91.6 ± 12.5  | 0.0316 ± 0.0026 | 0.9902 | 91.9 |
| Succinate | 7.41 ± 1.69 | 0 ± 98.7   | 0.0154 ± 0.0030 | 0.9728 | 46.9 |

4. Conclusion
Overall substrate conversion efficiency and hydrogen yield of *Rhodobacter sphaeroides* KKU-PS1 in the mixed substrates based on bio-succinate fermentation effluent were 17.4% and 1.31 mol H₂/mol mixed substrates, respectively. Growth, hydrogen production and substrate profiles were successfully represented by modified Gompertz, as well as by logistic model for growth. Cumulative hydrogen production and maximum hydrogen formation rate determined by Gompertz model were 1005 ml H₂/l and 4.1 ml H₂/l/h, respectively. *Rhodobacter sphaeroides* KKU-PS1 was able to grow and generate hydrogen well in mixed substrates based on bio-based succinate production effluent especially from xylose, succinate and glucose, highlighting the potential of utilizing the effluent for photofermentative hydrogen production. Further study using actual effluent from fermentative bio-succinate production is warranted for deeper understanding of possible inhibition sources in the effluent. Nevertheless, this study has provided insights on hydrogen producibility, growth, substrate consumption and associated kinetics involved in this process by *Rhodobacter sphaeroides* KKU-PS1 in mixed substrates, which altogether could serve as an important framework for future related studies.

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