# Co-Fermentation of Glucose and Xylose by *Gluconobacter oxydans* for Simultaneous Production of Gluconic and Xylonic Acids

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**Abstract.** Gluconic and xylonic acids are increasingly recognized as valuable bio-based chemical building blocks due to their broad applications in food, pharmaceutical, and polymer industries. These organic acids are primarily derived from the oxidation of glucose and xylose, respectively those two major monosaccharides commonly present in lignocellulosic hydrolysates. In this study, the oxidative bacterium *Gluconobacter oxydans* (*G.oxydans*) was evaluated for its co-fermentation potential to simultaneously convert glucose and xylose into gluconic and xylonic acids. The results revealed that *G.oxydans* effectively fermented xylose even in the presence of glucose, highlighting its flexible metabolic response. Notably, co-fermentation led to the accumulation of up to 94.8 ± 6.7 g/L xylonic acid, with glucose consumption partially inhibited during this process. Interestingly, the production profile shifted based on glucose concentration: low glucose levels (25 g/L) favored xylonic acid accumulation, while higher glucose concentrations significantly enhanced gluconic acid production, reaching 113.3 ± 0.7 g/L within 120 hours at an initial glucose concentration of 75 g/L. The transition between acid products suggests a substrate-regulated metabolic switch within *G.oxydans*. This observation demonstrates the bacterium's remarkable oxidative capacity and its suitability for valorizing sugar-rich feedstocks into multiple value-added products. The findings open avenues for developing efficient bioprocesses that simultaneously generate gluconic and xylonic acids, offering a sustainable route for integrated biorefinery applications.

**Keywords:** Co-fermentation, Gluconic acid, *Gluconobacter oxydans*, Xylonic acid.

## 1 Introduction

Agricultural products are always associated with lignocellulosic waste. The lignocellulosic waste consists of several polysaccharides such as cellulose, hemicellulose, and lignin [1]. Bioprocess technology has demonstrated significant potential in utilizing lignocellulosic waste to produce high-value chemical compounds. The utilization of waste generally involves the incorporation of microbes capable of converting simple sugar compounds from lignocellulose. Simple sugars derived from lignocellulose can take the form of glucose, a monomer of cellulose polysaccharides, and xylose, commonly found within hemicellulose [2][3].

Various chemical compounds such as gluconic acid, xylonic acid, and succinic acid are categorized as high-value building block chemicals. The utilization of lignocellulose to produce these chemical compounds involves various synthesis strategies. One of the most promising synthesis strategies is fermentation. Compared to other synthesis routes, such as electrolysis, photocatalysis, and others, the fermentation route proves advantageous in terms of synthesis simplicity, conversion efficiency, and energy requirements. A key strategy in fermentation is the selection of microbes capable of converting simple sugars. Like catalysts, microbes are the primary agents to transform monomeric sugars into valuable products. Fermentation operational conditions must align with the chosen microbes to effectively and efficiently drive product generation.

Following glucose, xylose is the most abundant sugar found in lignocellulosic biomass. Xylose are found in plant cell walls, commonly in the form of hemicellulose polysaccharides. Among various products resulted from xylose conversion, xylonic acid is one of the top 30 compounds with significant potential, based on the U.S. Department of Energy's evaluation [4]. Xylonic acid can be used as an alternative to gluconic acid and finds applications in various industrial fields. Apart from its role as a building block chemical, its utilization extends to industries like construction as a cement additive, agriculture as a bactericide and pesticide, and other uses such as glass and rust cleaners.

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S. C. Asih et al. (eds.), *Proceedings of the 19th International Conference on Quality in Research (QiR 2025)*, Advances in Engineering Research 303,
https://doi.org/10.2991/978-94-6239-717-0_17

Xylonic and gluconic acid can be readily produced by involving *Gluconobacter oxydans* (*G.oxydans*) because of the advantage over other fermentation bacteria capable of producing similar products because of its capacity to oxidize xylose, a bio-inert compound that is challenging to ferment. Another microorganism capable of gluconic acid production is *Aspergillus niger* (*A. niger*). However, the wild strain of *A.niger* lacks the ability to convert xylose and tends to form clumps during the fermentation process [5]. *G.oxydans* advantage in fermenting glucose and xylose provides a solution for producing gluconic acid and xylonic acid from various lignocellulosic waste. *G.oxydans* is commonly employed in the industrial sphere for large-scale gluconic acid production through fermentation thanks to its superior production capacity relative to other methods [6]. Techno-economic assessments of gluconic acid also underscore the potential of fermentation technology for enhanced profitability when contrasted with electrolysis techniques. Electrolysisconomic evaluation of gluconic acid synthesis via electrolysis yielded the lowest projected cost at approximately ±USD 1.5/kg [7]. Conversely, the techno-economic analysis of gluconic acid production through fermentation resulted in an estimated cost of around ±USD 0.4/kg [8]. However, it does have a relatively long synthesis time compared to thermal catalytic synthesis routes, photocatalysis, and electrodialysis [9]. The convenience and cost-effectiveness of this production approach have spurred further exploration into harnessing *G.oxydans* as a biocatalyst in xylonic acid manufacturing.

Despite extensive studies on single-substrate fermentations, limited research has focused on the simultaneous conversion of glucose and xylose, the two predominant sugars in lignocellulosic hydrolysates. Many conventional microorganisms preferentially consume glucose and repress xylose metabolism, reducing overall process efficiency. This poses a major challenge for integrated biorefineries, where co-utilization of mixed sugars is essential. In this study, we address this gap by evaluating the co-fermentation capability of *G.oxydans*, a bacterium with unique oxidative metabolism. By systematically varying glucose concentrations in the presence of xylose, we reveal substrate-dependent shifts between gluconic and xylonic acid production. This work highlights the biotechnological significance of harnessing *G.oxydans* for dual acid production from mixed sugar streams, providing new insights into co-fermentation strategies for sustainable bioprocessing.

# 1 Materials and Methods

## 1.1 Materials

The Gluconic acid measurement kits were bought from Megazyme®. Lithium xylonate was acquired from Merck™, while Glucose, Xylose, Ammonium sulphate, $KH_2PO_4$, and $MgSO_4.7H_2O$ were sourced from Wako. Tryptone and yeast extract were procured from Biokar diagnostics. All used chemicals are reagent grades.

## 1.2 Methods

**Strains and Media**

The culture media used in this study were formulated to support the growth and fermentation performance of *G.oxydans*. An agar medium was prepared for initial cultivation and colony isolation, while two inoculum media (Medium A and B) were designed with different glucose concentrations to evaluate growth responses during the pre-culture stage. Fermentation experiments were conducted using three distinct media (Medium C–E), which contained a fixed xylose concentration of 50 g/L and varying glucose concentrations of 25, 50, or 75 g/L. These levels were chosen to examine how substrate availability influences acid production: 25 g/L simulated limited glucose conditions to assess xylose utilization, 50 g/L represented a balanced carbon supply, and 75 g/L tested whether excess glucose would enhance gluconic acid production while repressing xylose metabolism. The selected concentrations also reflect sugar ratios commonly found in lignocellulosic hydrolysate. The detailed composition of all media is summarized in Table 1.

**Table 1.** Composition of culture media used in this study.

| Medium Type | Glucose (g/L) | Xylose (g/L) | $(NH_4)_2SO_4$ (g/L) | $KH_2PO$ (g/L) | $MgSO_4.7H_2O$ (g/L) | Tryptone (g/L) | Yeast Extract (g/L) | Agar (g/L) |
|---|---|---|---|---|---|---|---|---|
| Agar medium | 5 | - | - | - | 1.0 | 5 | 5 | 15 |
| Medium A | 10 | - | 1.5 | 1.5 | 0.5 | 5 | 20 | - |
| Medium B | 50 | - | 1.5 | 1.5 | 0.5 | 5 | 20 | - |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Medium C | 50 | 50 | 1.5 | 1.5 | 0.5 | 5 | 20 | - |
| Medium D | 25 | 50 | 1..5 | 1..5 | 0.5 | 5 | 20 | - |
| Medium E | 75 | 50 | 1.5 | 1.5 | 0.5 | 5 | 20 | - |

**Growth Conditions and Measurement**

The optical density was monitored for 72 h and measured at 600 nm ($OD_{600}$) to measure cell growth. Optical densities of whole cells were converted to Dry Cell Weight (DCW) as g DCW $L^{-1} = 0.319 \times OD_{600} - 0.0217$. DCW was measured using the gravimetric method, the samples were centrifuged and washed several times before dried at 80°C.

**Glucose and Xylose Fermentation**

*G.oxydans* were first rehydrated and cultivated in an agar medium. Agar cultures were incubated for three days at 30°C. To make an inoculum, a single colony was cultured in a shake flask culture at 200 rpm. The bacterial growth and gluconic acid production in inoculum culture were observed. The inoculum is harvested when they reach $OD_{600}$ 1 ± 0.1. A 10%(v/v) inoculum ratio is used as the fermentation starts with a total working volume of 500 ml at 30°C, 200 rpm for 120 h. Medium type C-E was used as the fermentation medium, and silicosen® was used as a flask stopper.

**Analytical Methods**

*Gluconic acid* is first measured using Megazyme™ reagent kits. The concentration of gluconic acid was calculated from a standard curve of concentration, which measures diluted sodium gluconate by UV-Vis spectrophotometer (Varian Cary 50 UV-Vis spectrophotometer, Agilent Technologies, USA) at 340 nm as instructed by the Megazyme™ kits manual. All samples were centrifuged at 6000 rpm for 10 min before adding reagents.

Samples were periodically taken, centrifuged, and filtrated through 0.45 µm PTFE filters before analysis. Gluconic and xylonic acid were analyzed using HPLC (UV-Vis detector UV-4075, Jasco, Tokyo, Japan) with Aminex HPX-87H column (Bio-rad, Hercules, CA, USA) at 50°C using the mobile phase of 5 mM $H_2SO_4$ at the flow rate of 0.25 ml/min. The detection wavelength was 210 nm.

**Statistical Methods**

All experiments were performed with n = 3 biological replicates unless otherwise stated. Statistical analysis was assessed using one-way ANOVA in Microsoft Excel, with a criterion of $p < 0.05$. Biological replicates refer to independent cultures initiated from separate inoculum, while technical replicates refer to repeated analytical measurements of the same sample. Technical replicates were averaged prior to calculating mean and SD for each biological replicate. No additional statistical hypothesis testing was performed; variability is represented by the SD to indicate reproducibility among replicates.

## 2 Results and Discussion

### 2.1 *Gluconobacter oxydans* Growth in Glucose Medium

Gluconic acid production and *G.oxydans* growth were evaluated in a synthetic medium. Fig. 1 shows *G.oxydans* growth is affected by glucose concentration in the medium. The strain preferred higher glucose concentration to boost its growth. Although the medium provides yeast extract as a secondary carbon source, glucose is the main factor that affects the growth levels. Previous studies have discovered that glucose could inhibit *G.oxydans* growth and reduce biomass concentration when the concentration is above 0.5 M[10]). *G.oxydans* are also able to grow by utilizing non-glucose carbon sources. A study compares several non-glucose carbon sources: xylose, arabinose, galactose, and mannose. 40 $gL^{-1}$ mannose produces the highest among all tested non-glucose sugar, reaching almost 1.4 $OD_{600}$ [11]. Our experiment shows that 10 $gL^{-1}$ glucose could yield 1.128 ± 0.055 $OD_{600}$ and 50 $gL^{-1}$ glucose could yield 2.750 ± 0.054 $OD_{600}$. It is aligned with the previous study, which stated the strain preference toward glucose as the fastest utilized carbon source [12].

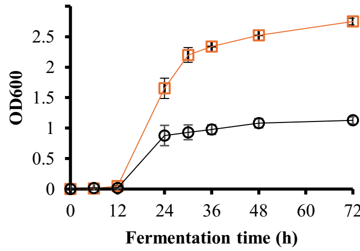



**Fig. 1.** $OD_{600}$ of *G.oxydans* in inoculum medium. ○: Medium A containing 10 $gL^{-1}$ glucose, □: Medium B containing 50 $gL^{-1}$ glucose.

Alongside its growth, *G.oxydans* also produces gluconic acid as the product of incomplete glucose oxidation. Membrane-bound alcohol dehydrogenase acts as the primary catalyst to produce extracellular aldonic acid [5]. The concentration of gluconic acid is affected by initial concentration and fermentation time, as shown in Fig. 2. The concentration reaches its peak during 24-36 h ($P<0.05$), where the growth of the cells is also significantly increased. However, the growth slowed and the concentration of gluconic acid decreased.

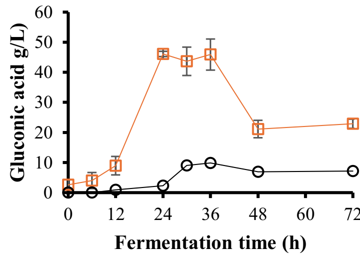



**Fig. 2.** Gluconic acid content in inoculum medium. ○: Medium A containing 10 $gL^{-1}$ glucose, □: Medium B containing 50 $gL^{-1}$ glucose.

The decrease in its concentration is mainly due to the further metabolism of the acid into its derivatives. Several studies have highlighted the conversion of gluconic acid into keto-gluconic acid during prolonged fermentation [8][11][13]. Fig. 1 and Fig. 2 indicate that the $OD_{600}$ increases slightly over the next 36-72 hours ($P<0.05$), followed by a significant reduction in gluconic acid concentration. We speculate that gluconic acid was partly consumed and converted into its derivatives that act as an inhibitor for growth. Zhou et al. (2018) demonstrates a cyclical fermentation using pelleted cells, the strategy proves that the reused cells were able to grow continuously [14]. These phenomena suggest that products could inhibit the cell. Although few have studied that *G.oxydans* can consume gluconic acid and keto-gluconate, consuming those metabolism products was not favored by *G.oxydans* [15][16].

These results indicate that *G.oxydans* prefers a high glucose concentration as its growth medium. It has a higher biomass yield and faster growth rate in a higher glucose content medium. As it grows on glucose, the strain produces gluconic acid and subsequently produces its derivative, which causes gluconic acid concentration to decrease.

### 2.2 Co-Fermentation of Glucose and Xylose

During shake flask fermentation, glucose and xylose are converted into gluconic and xylonic acids. *G.oxydans* growth in glucose and xylose medium is depicted in Fig.3. By lowering or increasing glucose concentration in the presence of 50 $gL^{-1}$ xylose, there were no significant differences in growth between each medium. *G.oxydans* was known to be able to grow by consuming various types of sugars, and its capability to consume xylose is desirable

for industries. Early experiments demonstrated the ability of the strain to grow in a xylose medium with the addition of 1 (g/g xylose) % glucose [17]. Other studies follow a similar strategy as glucose was considered a xylose-cofactor [18][19]. A study has discovered that *G.oxydans* could grow without the presence of glucose in the medium [20]. This proves that *G.oxydans* could grow in a pure xylose medium, albeit its growth rate is reduced [12]. Our experiment showed an increased growth rate and biomass yield when the glucose concentration was increased. However, with xylose addition, the growth rate between each medium is comparably similar. In fact, xylose may act as a substitute for glucose to support cell growth.

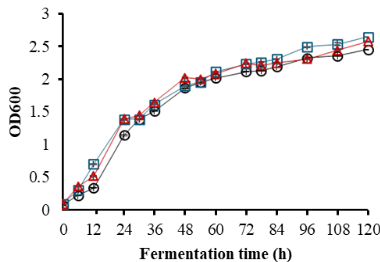
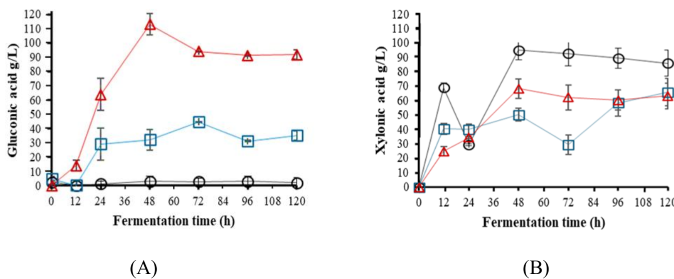



**Fig. 3.** $OD_{600}$ of *G.oxydans* in fermentation medium. O: medium C containing 50 $gL^{-1}$ glucose and 50$gL^{-1}$ xylose, □: medium D containing 25 $gL^{-1}$ glucose and 50 $gL^{-1}$ xylose, Δ: medium E containing 75 $gL^{-1}$ glucose and 50 $gL^{-1}$ xylose.

Xylonic acid and gluconic acid production during the fermentation process are shown in Fig. 4. The concentration of the acids was affected by initial concentrations of the corresponding monomeric sugar. The fermentation of 25 $gL^{-1}$ of glucose and xylose produces the highest xylonic acid concentration and no notable rise in gluconic acid concentration. Predominantly, the bacteria can produce xylonic acid when glucose is present. However, at the same time, gluconic acid is not always produced by *G.oxydans* when xylose is present. The strain was known to prefer glucose compared to other sources of carbon. Therefore, it is possible for the cell to consume glucose while also producing xylonic acid. Zhang et al. [20] showed a different result, where xylose was converted to xylonic acid after complete glucose consumption. The result may differ due to different starting concentrations and inhibitors in the fermentation broth. We found that gluconic acid is formed when glucose is available in large amounts, and xylonic acid is also formed during its fermentation.




(A) (B)

**Fig. 4.** A) gluconic and B) xylonic acid concentration in: O: medium C containing 25 $gL^{-1}$ glucose and 50$gL^{-1}$ xylose, □: medium D containing 50 $gL^{-1}$ glucose and 50 gL-1 xylose, Δ: medium E containing 75 $gL^{-1}$ glucose and 50 $gL^{-1}$ xylose.

Co-fermentation of glucose and xylose led to the accumulation of xylonic acid at 94.8 ± 6.7 $gL^{-1}$ when using medium C. The medium's low concentration of glucose may promote xylonic acid production. The gluconic acid reaches its highest concentration when using medium E, which contains the highest glucose concentration, reaching 113.3 ± 0.7 $gL^{-1}$. However, the concentration of xylonic acid is lower compared to co-fermentation with a low glucose medium. These results indicate that gluconic and xylonic co-fermentation is possible to be done. Xylose does not affect cell growth and will be converted to xylonic acid. Concurrently, the co-fermentation process also produces gluconic acid when the concentration is above 50 $gL^{-1}$. Compared with previous studies, the reported gluconic acid concentration was 240 g/L and xylonic acid was 66.42 g/L, which are lower than the values obtained in this study.

The dominance of gluconic acid at high glucose and the preference for xylonic acid when glucose is limited can be rationalized by the oxidative "periplasmic" metabolism of *G. oxydans* [23]. Glucose is oxidized primarily by the PQQ-dependent (Pyrroloquinoline Quinone) membrane-bound glucose dehydrogenase (mGDH) to gluconate, and then further converted into keto-gluconates through highly active periplasmic dehydrogenases, which outcompete cytosolic routes and control flux by direct electron transfer to the respiratory chain. Under batch conditions, mGDH activity predominates over soluble NAD(P)-linked GDH, favoring rapid gluconate formation when glucose is abundant [24][25].

Xylose conversion to xylonate proceeds via membrane-bound xylose dehydrogenase to xylonolactone/xylonate. Genetic studies in *G.oxydans* 621H indicate multiple, partially redundant enzymes and unclear xylulose-kinase steps; notably, perturbing mGDH or PQQ availability can also impact growth or xylonate accumulation, suggesting that competition for PQQ cofactor and respiratory capacity modulate flux between glucose and xylose oxidation [25]. This provides a plausible basis for the observed "switch": high glucose loads channel PQQ-dependent electron flow toward mGDH and gluconate, whereas lower glucose allows more effective xylose oxidation and xylonate build-up [27]. Consistent with this view, engineering that increases mGDH expression elevates oxidative fluxes and can reshape product profiles (e.g., strengthened tolerance and xylonic-acid productivity in engineered strains), while classic physiology shows that mGDH activity is a key rate-determining step for gluconate formation.

## 3 Limitations and Future Direction

While this work demonstrates the feasibility of simultaneous gluconic and xylonic acid production by G. oxydans, several limitations remain. Substrate inhibition was evident, as high glucose levels promoted gluconic acid formation but repressed xylose utilization, suggesting that batch fermentation may not fully support balanced co-production. The study was also limited to shake-flask conditions, where oxygen transfer and pH control differ from industrial reactors, and metabolic profiling was restricted to extracellular acids without enzyme- or gene-level insights. Future work should address these challenges by testing fed-batch or oxygen-enriched strategies, applying in-situ product removal, and exploring metabolic engineering such as overexpressing xylose dehydrogenase or modulating PQQ-dependent glucose dehydrogenase. Adaptive evolution and omics analyses could further enhance tolerance, clarify regulatory mechanisms, and guide the development of strains optimized for large-scale dual acid production.

## 4 Conclusion

Co-fermentation of glucose and xylose can produce gluconic and xylonic acid simultaneously. *G.oxydans* prefer to consume glucose compared to xylose, which causes a decrease in gluconic acid concentration during prolonged fermentation. Fermentation using a medium with high glucose content can produce 113.3 ± 0.7 gL-1 gluconic acid in 48 h while also producing 68.1 ± 0.7 gL-1 xylonic acid. However, a low glucose medium will not produce gluconic acid in the presence of xylose. The results also proved that xylose is not an inhibitor of cell growth, although its utilization is slower than glucose.

**Acknowledgments.** The authors would like to express their sincere gratitude to the Laboratory for Environment and Life Science, Tokyo University of Agriculture and Technology for providing essential facilities, technical support, and a conducive research environment throughout the course of this study. The laboratory's contribution was instrumental in enabling the successful execution of the experimental work and data analysis presented in this research.

**Disclosure of Interests.** The authors declare that they have no competing interests that are relevant to the content of this article.

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