Metabolism and Bioconversion of PET Monomers

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Polyethylene terephthalate (PET) is a widely used plastic that is polymerized by terephthalic acid (TPA) and ethylene glycol (EG). Pseudomonas sp., and E. coli have ability to utilize EG. In A. woodii, EG can be utilized by an acetaldehyde/ethanol pathway while it is consumed by a glyoxylic acid pathway in Pseudomonas sp. and E. coli.

Polyethylene terephthalate | Ethylene Glycol | Metabolism | Terephthalic acid

1. Metabolism of Ethylene Glycol (EG)

At present, two naturally existing pathways, including the acetaldehyde/ethanol pathway and glyoxylic acid pathway for the utilization of EG by microorganisms, have been reported. The use of EG is not commonly reported in metabolic engineering of model microorganisms, except for *E. coli*.

1.1. Acetaldehyde/Ethanol Pathway

The acetogenic bacterium *A. woodii* can use EG as the sole carbon source for growth, and the EG metabolic pathway has been identified [1]. EG is dehydrated to acetaldehyde, catalyzed by the propane diol dehydratase (PduCDE), then further converted into ethanol and acetyl coenzyme A (acetyl-CoA), catalyzed by CoA-dependent propionaldehyde dehydrogenase (PduP) [2]. PduCDE and PduP are both encoded by the Pdu gene cluster [2]. Acetyl-CoA and a part of the ethanol are converted into acetic acid, and this process is accompanied by the production of adenosine triphosphate (ATP) and nicotinamide adenine dinucleotide (NADH) [2]. The reducing equivalents of the ethanol oxidation are recycled through the reduction of carbon dioxide (CO_2) into acetate in the Wood–Ljungdahl pathway [1]. The acetaldehyde/ethanol pathway is commonly found in some Clostridium species and a few other anaerobic organisms because the enzymes that catalyze EG are oxygen sensitive. Additionally, Dragan et al. [1] and Nilanjan et al. [3] proved that the enzymes for EG utilization were encapsulated in bacterial microcompartments.

1.2. Glyoxylic Acid Pathway

Glyoxylic Acid Pathway in *Pseudomonas sp.*

In *Pseudomonas aeruginosa* and *Pseudomonas putida*, EG is converted into glyoxylic acid under the action of dehydrogenase and finally enters the TCA cycle through different routes [4][5][6][7]. At present, the metabolic

pathway of EG in *P. putida* KT2440 is the most widely studied. The metabolism pathways in utilizing EG have been well demonstrated in *P. putida* KT2440, in comparison to other bacteria, and related enzymes have been identified. In *P. putida* KT2440, two functionally redundant periplasmic quinoproteins, PedE and PedH, catalyze EG into glycolaldehyde [8]. PedE and PedH are both pyrroloquinoline quinone-dependent alcohol dehydrogenases (PQQ-ADHs), and their expression depend on Ca^{2+} and lanthanide metal ions, respectively [8]. Once glycolaldehyde is produced, the two cytoplasmic aldehyde dehydrogenases, PP_0545 and PedI, catalyze it into glycolic acid, and glyoxylic acid is further generated via the membrane anchored oxidase GlcDEF. The glyoxylic acid is converted into acetyl-CoA and enters the TCA cycle to be catalyzed by a series of enzymes [9]. Additionally, there are another two alternative pathways to convert glyoxylic acid, one of which is catalyzed by isocitrate lyase (AceA) and glyoxylic acid can condense with succinic acid to form isocitrate. The other is catalyzed by malate synthase (GlcB) and glyoxylic acid condenses with acetyl-CoA to form malic acid. However, due to the removal of CO_2 and the restriction of the amount of acetyl-CoA, *P. putida* KT2440 cannot use EG as the sole carbon source for growth [9]. Researchers engineered *P. putida* KT2440 by overexpressing glycolate oxidase to remove the glycolate metabolic bottleneck and produced an engineered strain that can efficiently metabolize EG [9]. After that, mutants of *P. putida* KT2440 that utilize EG as the sole carbon source were isolated through adaptive laboratory evolution, and the metabolism and regulation mechanism of EG in *P. putida* KT2440 was further clarified [10]. *P. putida* JM37 was reported to be able to use EG as the sole carbon source for growth because there is another pathway to use glyoxylic acid compared to *P. putida* KT2440. Glyoxylic acid is converted into tartrate semialdehyde under the catalysis of glyoxylate carboxylase (Gcl) and then tartrate semialdehyde is converted into glycerate acid, catalyzed by hydroxypyruvate isomerase (Hyi) and tartrate semialdehyde reductase (GlxR). Glycerate acid can be further converted into 2-phosphoglycerate and enter the TCA cycle [11].

Glyoxylic Acid Pathway in *E. coli*

Wild-type *E. coli* cannot use EG as the sole carbon source for growth [12]. In 1983, researchers first reported an *E. coli* strain capable of using EG as the sole carbon source from the propylene glycol using mutants. They identified the increased activities of propanediol oxidoreductase, glycolaldehyde dehydrogenase, and glycolate oxidase in the mutants [12]. Based on this discovery, researchers began to design and construct engineered *E. coli* that could use EG to convert PET monomers into high value chemicals.

EG is assimilated and oxidized into glycolaldehyde and, subsequently, into glycolic acid under the catalysis of 1,2-propanediol oxidoreductase mutant (fucO) and glycolaldehyde dehydrogenase (aldA), respectively. Glycolic acid can be metabolized into glyoxylic acid by glycolate dehydrogenase (GlcDEF) [13]. Similar to *P. putida*, glyoxylic acid is further condensed into acetyl-CoA by the linear glycerate pathway or converted into isocitrate and malate catalyzed by AceA and GlcB, respectively. An engineered *E. coli* can take EG as the sole carbon source to produce glycolate by expressing fucO mutant (I7L/L8V) and aldA. Experiments identified that oxygen concentration was as an important metabolic valve, and flux to 2-phosphoglycerate was the primary route in the assimilation of EG as a substrate combining modeling [7][14]. Additionally, EG can be efficiently utilized in *E. coli* by optimizing the gene expression (fucO and aldA) and adding a growth medium with a low concentration of glycerol or a mixture of amino acids [13]. Although *E. coli* MG1655 contains the endogenous glyoxylic acid metabolism pathway, the EG-utilizing

ability of the engineered *E. coli* still needs to be improved [14]. Introducing a heterologous pathway or unblocking the rate-limiting steps of the EG metabolic pathway in *E. coli* may further enhance the assimilation of EG. *E. coli* has a clear genetic background and simple genetic operations compared to other bacteria, so it is easier to engineer it to transform EG into high value chemicals.

2. Bioconversion of EG to High Value Chemicals

EG is one of the cheap raw materials for glycolic acid production through incomplete oxidation. Several wild microorganisms, including *Pichia naganishii* [6], *Rhodotorula sp.* [6], *Burkholderia sp.* [15], *Gluconobacter oxydans* [16], and *Hansenula sp.* [17], have been reported to produce glycolic acid from EG. Among these microorganisms, *G. oxydans* has been extensively studied due to its high titer of glycolic acid from EG. It is reported that the overexpression of membrane-bound alcohol dehydrogenase (mADH) in *G. oxydans* DSM 2003 accelerated cell growth, and 113.8 g/L of glycolic acid was accumulated with a molar yield of 92.9% within 45 h [18]. Two genes encoding recombinant cytosolic oxidoreductases (gox0313 and gox0646) from *G. oxydans* were heterologously expressed in *E. coli* and the resulting proteins were purified and characterized [19]. In addition to *G. oxydans*, engineered *E. coli* has potential in producing glycolic acid from EG, and 10.4 g/L of glycolic acid was produced from EG after 112 h in a fed-batch bioreactor using a series of oxygen-based strategies [13][12].

EG can also be used to produce polyhydroxyalkanoate (PHA) by *P. putida* under nitrogen-limiting conditions [20]. An engineered strain *P. putida* KT2440 realized the conversion of EG into mcl-PHAs [9][20] and some metabolic engineering strategies were developed to enhance medium chain length polyhydroxyalkanoates (mcl-PHAs) production in *P. putida* [21][22][23]. mcl-PHAs can be upgraded into chemical precursors and fuels via a straightforward catalytic process [24].

3. Metabolism of TPA

It was reported that *Comamonas sp*. [25], *Delftia tsuruhatensis* [26], *Comamonas testosterone* [27], and *Rhodococcus sp*. [28] can use TPA as the sole carbon source for their growth. In these bacteria, TPA enters the cell via the TPA transporters [29]. Generally, TPA can be transformed into 1,6-dihydroxycyclohexa-2,4-diene-dicarboxylate (DCD) under the catalysis of TPA dioxygenase (TphAabc), and DCD is further oxidized by 1,2-dihydroxy-3,5-cyclohexadiene-1,4-dicarboxylate dehydrogenase (TphB) to form protocatechuate (PCA) [27][30][31][32]. The genes responsible for these reactions have been characterized [25][28][26][27]. *Comamonas sp*. E6 also contains the extra gene TphC, which encodes a permease involved in TPA uptake using the tripartite aromatic acid transporter [29]. There are three main pathways for the metabolism of PCA, the ortho-, meta-, and para-cleavage pathways, which are catalyzed by 3,4-dioxygenase (PCDO), 4,5-dioxygenase, and 2,3-dioxygenase, respectively [33][34][35][36]. At present, the ortho-cleavage pathway is the most extensively studied, and PCA is converted into β-carboxymuconate under the catalysis of protocatechuate 3,4-dioxygenase (PCDO), is finally converted into acetyl-CoA, and enters the TCA cycle [33][37].

4. Bioconversion of TPA to High Value Chemicals

It has been demonstrated that the PET monomer TPA is suitable for the biosynthesis of several high value chemicals, such as gallic acid, pyrogallol, catechol, muconic acid, vanillic acid, catechol, adipic acid, PHA, and β-ketoadipic acid [38][39][40][41][42][43]. Since PCA is an important precursor in producing a series of high value aromatic chemicals, the key to the bioconversion of TPA is the acquisition of PCA. By the heterologous expression of TPA, 1,2-dioxygenase (TphAabc), and DCD dehydrogenase (TphB) from *Comamonas sp.*, *E. coli* was engineered to utilize TPA and produced PCA [32]. Further heterologous expression of different enzymes produced gallic acid, pyrogallol, catechol, muconic acid and vanillic acid from PCA in *E. coli* [32]. Additionally, a novel pathway for the direct upcycling of TPA into the value-added small molecule vanillin was reported in engineered *E. coli* and the conversion efficiency reached 79% [43].

PHA can also be produced from TPA. Researchers have isolated *P. putida* GO16 and *P. putida* GO19 from a PET bottle processing plant and proved their ability to convert TPA into PHA at a maximal rate of approximately 8.4 $mg{\cdot}L^{-1}{\cdot}h^{-1}$ for 12 h [44]. Recently, researchers engineered *Pseudomonas umsongensis* GO16 to convert PET into two types of bioplastics, PHA and a novel bio-based poly (amide urethane) (bio-PU), and further achieved the secretion of hydroxyalkanoyloxy alkanoates (HAAs) by introducing the HAA synthesis module into the engineered strain [45]. Poly-(R)-3-hydroxybutyrate (PHB), the first PHA discovered, has also been produced from PET through the heterologous expression of the phbCAB operon from *Ralstonia eutropha* in *Pseudomonas stutzeri* [38]. Due to the same synthetic precursors of rhamnolipids and PHA, many microorganisms capable of converting PET into PHA also have the potential to synthesize rhamnolipids [44]. The conversion of PET into biodegradable plastics is a clean and cost-effective way to generate a great market in PET recycling [46].

As for producing β-ketoadipic acid from TPA, four sequential metabolic engineering efforts in *P. putida* KT2440 were performed to directly convert BHET into β-ketoadipic acid [39]. The engineered *P. putida* is able to not only degrade BHET into TPA and EG, but also convert TPA into 15.1 g/L of β-ketoadipic acid at 76% molar yield in bioreactors [39]. β-ketoadipic can be further polymerized into a nylon-6,6 analog, or other products [47].

PET waste is depolymerized by microorganisms in nature and converted into CO_2 and water, which causes serious resource loss and carbon emissions. Therefore, utilizing PET and its monomers to produce high value chemicals provides a new solution for upgrading and recycling PET and other plastics waste [48].

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