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Review article

Sustainable bioconversion of synthetic plastic wastes to polyhydroxyalkanoate (PHA) bioplastics: recent advances and challenges

Abstract

Millions of tons of chemical plastics are accumulated annually worldwide in terrestrial and marine environments due to inadequate recycling plants and facilities and low circular use. Their continuous accumulation and contamination of soil and water pose a severe threat to the environment and to human, animal and plant health. There is therefore an urgent need to develop effective eco-environmental strategies to overcome the significant environmental impacts of traditional plastic waste management practises (incineration, landfilling, and recycling). In recent years, reports on microbial strains equipped with the potential of degrading plastic materials, which can further be converted into usable products such as PHA bioplastics have sprung up, and these offer a possibility to develop microbial and enzymatic technologies for plastic waste treatment and then progressing plastics circularity. In this chapter, an overview of the reported microbial and enzymatic degradations of petroleum-based synthetic plastics, specifically polyethylene, polystyrene, polypropylene, polyvinyl chloride, polyurethane and polyethylene terephthalate, is detailed. Furthermore, the harvesting of depolymerization products to produce new PHA materials with high added industrial value can be considered as an innovative solution, helping to increase synthetic plastic recycling rate and creating new circular economy opportunities. Finally, the challenge of ending plastic pollution is still difficult, but sustainable, renewable, bio-based and completely biodegradable, PHA will hold enormous promise for replacing plastics made from petrochemicals.

Keywords: polyhydroxyalkanoates, renewable feedstock, biodegradation, bioconversion, plastic wastes, microorganisms, enzymes

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Introduction

Plastics are long chains polymeric molecules composed of repetitive units synthesized by polymerization, polycondensation or polyaddition reactions from hydrocarbons and petroleum derivatives.[1,2] Conventional plastic denotes a vast family of materials. The most communal synthetic polymers are polypropylene (PP); polyethylene (PE), polystyrene (PS), polyethylene terephthalate (PET), polyvinyl chloride (PVC) and polyurethane (PU, PUR) and the most consumed synthetic polymer is PE.[3–5] These materials exhibit various properties such as stability, durability, low cost, high elasticity, robustness, light-weight and tensile strength.[6,7] Owing to the outstanding properties, plastics are widely used product in many areas of daily life and industry worldwide.[5,8,9] Due to extensively use and growing demand of synthetic plastics in many industrial sectors, production of petroleum-based plastics is increasing steadily.[9,10] Indeed, the worldwide annual plastic production reached 390.7 million tonnes in 2021 and is expected to exceed 34 billion tonnes by 2050.[11,12] Furthermore, the massive use of single-use disposable plastics such as face masks, gloves, and other personal equipment in COVID-19 pandemic has caused a sharp increase in plastic wastes which is estimated at 1.6 million tonnes per day.[13–15] Accordingly, the high plastic production generates millions of tonnes of plastics wastes that ended up in landfills and marine environments, resulting environmental pollution.[16–18] Recycling, landfilling, as well as incineration are the methods used for waste plastic management to reduce plastic's environmental impacts.[3] Nevertheless, these methods are costly, requires huge amounts of energy, are not sufficient and often generate harmful secondary pollutants.[19,20] Furthermore, only less than 10% of plastic wastes are recycled, and more than 80% of plastic are accumulating in the environment.[18] Moreover, due to the macromolecular structure, stability, hydrophobicity of synthetic plastics, they are mostly non-biodegradable and have a slow rate of degradation under natural environment conditions and persist in the environment.[21,22] Therefore, the tremendous accumulation of plastic wastes as well as the improperly appropriate waste plastic management led to water and land pollution and poses severe environmental threats to the terrestrial and marine ecosystems.[9,23] Hence, there is a need for the development of an effective and sustainable solution for efficient management of petroleum-based plastic wastes to mitigate environmental plastic pollution.[24] Microbial degradation is a promising solution that catalyzes the breakdown of polymers by specific enzymes into monomers, oligomers that can be further used as carbon source for bacterial growth.[8,25] Plastic biodegradation using different microorganisms and enzymes have been reported.[26–29] Several studies have been conducted on the ability of bacterial strains to degrade conventional plastics as well as the metabolic pathways related to their degradation.[25,30,31] Petroleum-based plastics biodegradation depends on the nature of the bonds in the polymeric chains. Indeed, PET and PUR, which have hydrolysable ester bonds in their backbones, are more biodegradable than PE, PS, PP, and PVC, which have carbon chain backbones.[26] Recently, valorization of plastic biodegradation products to produce value-added products such as polyhydroxyalkanoates (PHA) opens up new opportunities for waste management strategies in a circular economy approach.[26,32] PHA are a family of biodegradable polymers synthesized by different microorganisms as intracellular energy and carbon storage materials under nutrients or oxygen limitation.[33,34] The utilization of plastics degradation products for the production of PHA contributes for the decrease in waste plastics as well as in the production of biodegradable plastics.

In this review, we summarize bacterial degradation of various types of synthetic plastics such as PE, PET, PU, PVC, PS and PP as well as the most enzymes that might be involved in metabolic pathways related to plastics degradation. Furthermore, we discuss the bioconversion of plastics into PHA.

I. Bacterial and enzymatic degradation of synthetic plastic

Biodegradation of plastics is the most effective solution for sustainable environmental waste plastics management. Degradation of synthetic plastics by microorganism consists in the breakdown of complex polymers by specific enzymes into smaller molecules e.g., oligomers, dimers, and monomers (Figure 1).[8,23] Many factors might affect plastic degradation process such as high molecular weight, chemical composition, crystallinity, hydrophobicity.[8,35,36] During plastic polymer biodegradation, microorganisms first adhere into the surface of plastic films by the excretion of enzymes which are involved in fragmentation and hydrolysis of polymers. Fragments released are further assimilated by bacterial cells and metabolized to be converted to microbial biomass.[23,26,37] Various microorganisms have been conducted to degrade synthetic plastics and pretreated plastics. Plastics are divided into two groups according to the nature of bonds in their backbones. Indeed, PS, PP, PE and PVC plastics have carbon-carbon (C-C) bonds in their structure. They are recalcitrant to biodegradation due to the absence of hydrolysable functional groups in their backbones and the extremely stable C-C bonds. Even though plastics are extensively used, there are only a few reports on their effective biodegradability.[30,38] While PET and PU have an heteroatomic backbone in their structure. They are more susceptible to biodegradation due to presence of hydrolysable functional groups.[25,26,30,39]

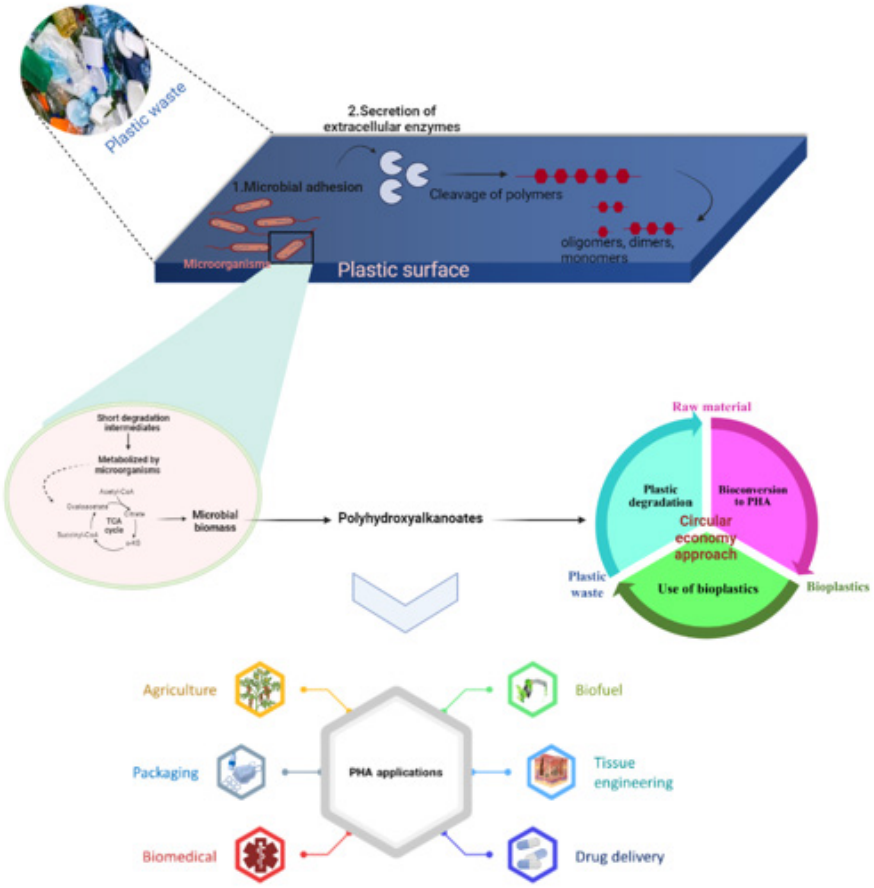

Figure 1 Exploring bio circular economic design opportunities: from plastic waste to PHA.

Degradation of plastics with heteroatomic backbone

Polyethylene terephthalate (PET)

PET mechanism biodegradation

Polyethylene terephthalate is one of the most used and synthesized petrochemical-plastics that is produced in enormous quantities worldwide.[26,37] PET is composed of repeating units of terephthalic acid (TPA) and ethylene glycol (EG) monomers through ester bonds forming a semi aromatic thermoplastic polymer.[7,12,40] The physiochemical properties and low price of PET result in diverse applications especially in packaging industries.[7,37]

Because of its high production and excess use, PET presents a major waste problem.[41] Considering biodegradation as an eco-friendly approach, several bacterial species have demonstrated their capacity to degrade PET.[35]

PET is the most studied polymer in terms of biodegradation.[12] The degradation of PET release components and degradation products include TPA, EG, MHET and Bis-(2-hydroxyethyl) terephthalate (BHET) under the action of hydrolases enzymes which degrade the

ester bonds.[40] Among these products, PETase can hydrolyze BHET to produce MHET, TPA, and EG. Furthermore, MHET could be further degraded into TPA and EG by the action of MHETase.[40]

These degradation products can be used by different microorganisms and metabolized through different metabolic pathways as energy sources, entering the tricarboxylic acid cycle (TCA cycle) or converted into high value chemicals (Figure 2).[26,29,40]

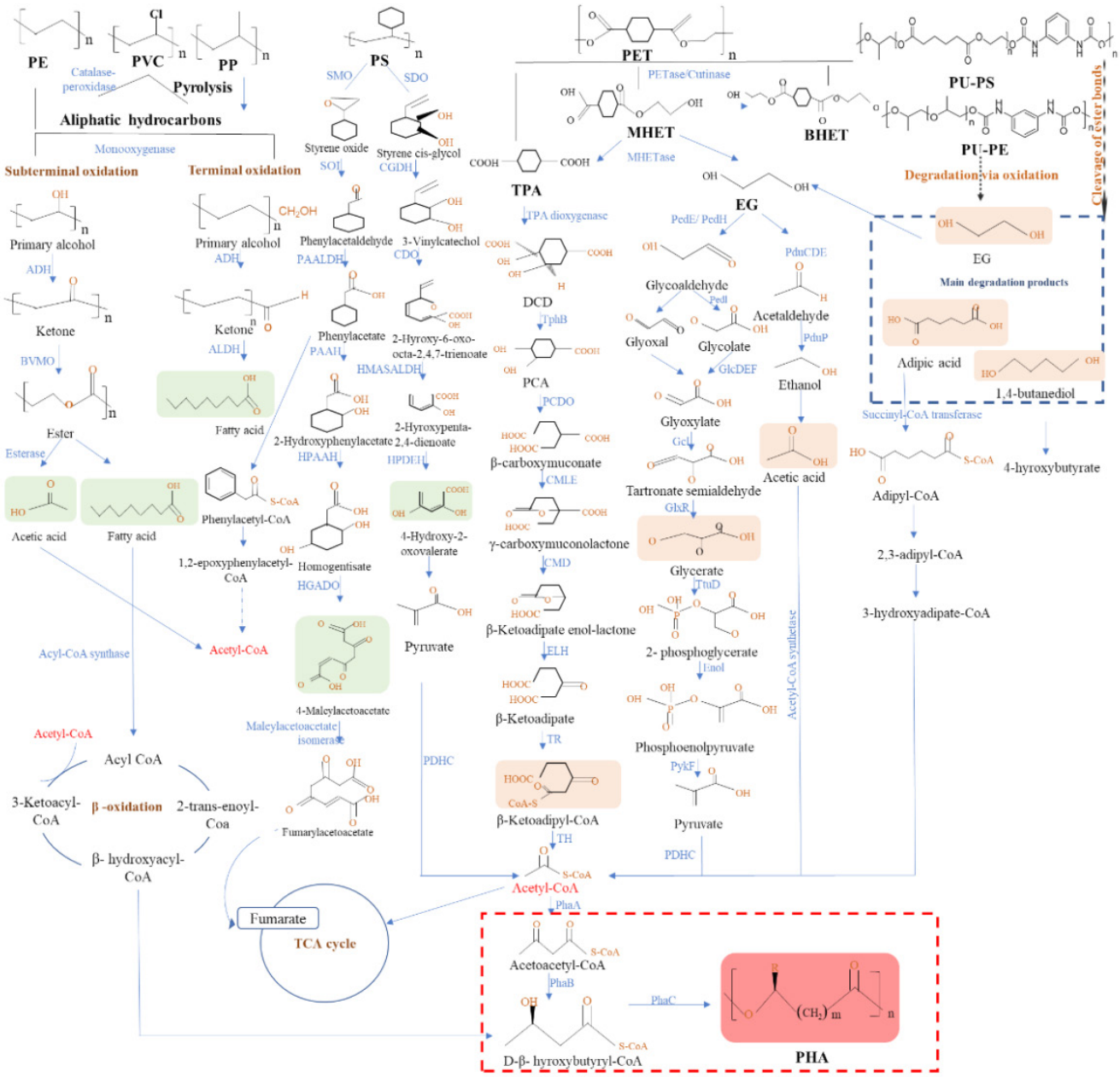

Figure 2 Biodegradation and bioconversion pathways of synthetic plastics into bioplastics.

TPA can be converted by the activity of TPA dioxygenase producing 1,6-dihydroxycyclohexa-2,4-diene-dicarboxylate (DCD) which is then oxidized to protocatechuate (PCA) under the action of 1,2-dihydroxy-3,5-cyclohexadiene-1,4- dicarboxylate dehydrogenase (TphB). PCA is further undergo dioxygenolytic cleavage through successive reactions to form acetyl-CoA and then enters the tricarboxylic acid (TCA) cycle.[26,29,40,42]

Several studies have reported the degradation of PET (Table 1). For instance, *Comamonas* sp.,[43] *Rhodococcus* sp. strain DK17,[44] *Delftia tsuruhatensis,*[45] *Ideonella sakaiensis* 201-F6,[46] *Bacillus subtilis*.[47]

Also, EG could be assimilated through two pathways. Indeed, it can be degraded to acetaldehyde by PduCDE and then to ethanol which is eventually transformed to acetate.[40] For instance, *Acetobacterium woodii* transform EG to ethanol in which it converted to acetate.[48]

Moreover, EG can be oxidized to glycerate by a series of enzymes. In fact, EG is oxidized to glycoaldehyde, then it can be converted into glycolate which can be catalyzed by glycolate oxidase to generate glyoxylate. Afterwards, acetyl-CoA is produced through glycerate pathway and enters TCA cycle.[23]

Several microorganisms capable of metabolizing EG have been identified such as *A. Woodie,*[48] *Pseudomonas putida* KT2440,[49] *P. putida* strain JM37.[50]

PET degrading enzymes

Largest number of PET-hydrolyzing enzymes are identified and characterized by various microorganisms. These include lipases, cutinases, esterases.[8,7,40,41] PET hydrolase (PETase) catalyzes the breaking of the PET polymer through the hydrolysis of ester bonds[40,51] into terephthalate acid (TPA), EG, bis(2-hyroxyethyl) terephthalate (BHET), and (mono-(2-hydroxyehyl)terephthalic) acid (MHET).[12]

To date, more than 24 different PET hydrolases enzymes have been identified.[12] Such as PETase (EC 3.1.1.101) was discovered from the bacterium *Ideonella sakaiensis* 201-F6 by Yoshida et al.[46] It was found to produce the enzymes PETase and MHETase, which can break down PET into intermediate products that can be metabolically assimilated. The discovery of these enzymes is advantageous in achieving high PET biodegradation efficiency. Further high activity hydrolases variations have emerged as a result of significant study being done on the structures of these two enzymes.[40] Also, a cutinase PET degrading enzyme from *Thermobifida fusca* (TfC),[52] Cut190 from *Saccharomonospora viridis* AHK190,[53] cutinase from *T. alba* (Tha_Cut1)[54] and from *P. mendocina*.[55] TfHCut, *Thermomonospora fusca* hydrolase, characterized as a thermophilic hydrolase with ability to degrade PET. Another enzyme expressed by *T. fusca* showed PET degradation is BTA Hydrolase-2 (BTA-2) (12). Only a few esterases such as p-nitrobenzylesterase from *Bacillus subtilis* (BsEstB)[56] and a carboxylic ester hydrolase from the marine bacterium *P. aestusnigri.*[57] Many lipases can hydrolyze PET as well, but their activity is low. Compared to esters hydrolyzed by lipases, esters having a shorter chain aliphatic region are typically hydrolyzed by esterases.[58]

The hydrolytic activity of all these enzymes is required at high temperature. This feature is advantageous for PET degradation, because of the glass transition temperature of PET is about 75°C. However, biodegradation of PET by *I. sakaiensis* can also occur at lower temperatures.[57] The PET hydrolases identified have poor stability and low activity, which limit their large-scale industrial application.[40] In order to enhance the catalytic activity of PETase, researchers have mainly focused on the production of mutant form of PETase through protein engineering.[59]

Polyurethanes (PU)

PU mechanism biodegradation

Polyurethanes are an important and versatile family of plastics polymers. They are the 6th most abundant synthetic polymer material.[60] They are widely used in several industries as raw materials in many products including furniture, coating, construction materials, fibers, and paints, as well as in flexible foams and absorbents for many end-user products.[26,60–62]

PU, which are characterized by urethane bonds, are produced by reaction between aliphatic or aromatic polyisocyanate and hydroxyl groups of polyols (typically a small-molecule diol or a diamine).[61–63] PU is produced from a wide range of starting materials, depending on the isocyanate and polyol composition, it leads to an enormous diversity of PU products.[62,63] Based on the polyols used, PU can be divided into two major types: polyester-polyurethane (PS-PU) and polyether-polyurethane (PE-PU).[64]

The majority of PU materials are specifically synthesized to guarantee long-term durability and resistance.[60] Polyester PU are considered to be relatively vulnerable to microbial degradation.[64]

The study of PU biodegradation is a burgeoning area of research since it helps with the creation of environmentally friendly materials.[36] Several parameters determine PU degradability and impact the mechanism of enzymatic degradation such as process conditions, morphology, chemical groups present in the polymer which determine the accessibility to degrading enzyme, crystallinity, hard and soft segment ratio.[65] The detailed biodegradation mechanisms dependent on the chemical structure of PU. It dependent on the prepolymer is polyester or a polyether. In which, PS-PU is relatively vulnerable to microbial attack, ester groups in the soft-chain segments it is typically susceptible to hydrolytic breakdown under the action of Esterase resulting in the release of carboxylic acid and alcohol terminal groups.[64] PE-PU is significantly more stable than PS-PU, and the ether group is more resistant to hydrolysis than the ester group.[29] Hence, oxidation is the primary mechanism through which PE-PU biodegradation takes place (Figure 2).[64] The biodegradation products of PU are derived from polyester segment when ester bonds are hydrolyzed and cleaved indicated that the polyurethane biodegradation was due to the hydrolysis of only ester bonds, presenting 'false positive' results.[64,66]

The discovery of PU-degrading bacteria and related enzymes have been studied.[64,67] The literature reports some microorganisms having the ability to degrade polyurethane (Table 1) such as *Bacillus subtilis* strain MZA-75 can degrade the soft segment of polyester polyurethane,[68] *B. subtilis.*[47] A soil microorganism, *Acinetobacter gerneri* P7, was investigated for its ability to degrade PU.[69] The most investigated genus is *Pseudomonas*.[36,70] Indeed, *P. protegens* Pf-5 and *P. aeruginosa* MZA-85 are described as polyester polyurethane degrading.[68,70] Peng et al. (2014)[71] reported the capacity of *P. putida* to degrade 92 % of Impranil DLN in 4 days. Also, it has been observed that *P. aeruginosa* is able to degrade Impranil DLN.[72] Also, degradation by microbial communities is elaborated.[36] However, the biodegradation efficiency of PU-PE was significantly lower than PU-PS, and few microorganisms were elaborated to degrade PU-PE.[67]

Table 1 Reported Plastic degrading microorganisms

Strains	Plastic Type	Incubation time	Weight loss (WL) (%)	Techniques used	References
Heteroatomic backbone					
Pseudomonas sp.AKS2	LDPE films collected from local markets	45 days	5%	NM	117
Microbacterium paraoxydans *P. aeruginosa*	LDPE	2 months	61.00% 50.50%	FTIR-ATR, WL	178

Table 1 Continued...

Strains	Plastic Type	Incubation time	Weight loss (WL) (%)	Techniques used	References
Heteroatomic backbone					
Rhodococcus ruber C208	LDPE Ipiten 111	2 months	7.50%	SEM, WL	179
Acinetobacter baumannii	LDPE	30 days	NM	FTIR, GC-MS	180
Cobetia sp. Halomonas sp. Exigobacterium sp. Alcanivorax sp.	LDPE	90 days	1.4% 1.72% 1.26% 0.97%	FE-SEM, ATR-FTIR, AFM, TGA	181
B. amyloliquefaciens BSM-1 B. amyloliquefaciens BSM-2	LDPE	60 days	11% 16%	SEM, FTIR, WL	87
Bacillus sp. ISJ55	LDPE	60 days	1.50%	SEM, FTIR, WL	182
Ralstonia sp. *strain* SKM2 *Bacillus* sp. *strain* SM1	LDPE	180 days	39.2% 18.9%	WL, FTIR, alteration of pH	183
Brevibaccillus borstelensis	LDPE	30 days	11%	WL, FTIR	184
P. aeruginosa SKN1	LDPE strips	60 days	10.32%	FTIR, SEM	185
Klebsiella pneumoniae CH001	HDPE	60 days	18.40%	FTIR, SEM, AFM, WL	186
Pseudomonas sp. *Arthrobacter* sp.	HDPE	30 days	15% 12%	WL, FTIR	187
Enterobacter asburiae YT1 Bacillus sp. YP1	PE	60 days	6.1% 10.7%	SEM, AFM, XPS, micro-ATR/FTIR	109
Bacillus sp. and *Paenibacillus* sp.	PE	60 days	14.70%	SEM, WL, GC-MS, TGA, FTIR	188
B. cereus	PE	40 days	1.60%	SEM, WL, FTIR	108
B. gottheilii			6.20%		
B. subtilis	PE	30 days	9.26%	WL, FTIR	189
Enterobacter sp. D1	PE	31 days	NM	SEM, AFM, FTIR, LC-MS	190
Bacillus sp.	High Impact PS	30 days	23%	WL, SEM, HPLC, NMR, FTIR, TGA	191
Enterobacter sp., *Citrobacter sedlakii*, *Alcaligenes sp.* and *Brevundimonas diminuta*	High Impact PS	30 days	12.40%	FTIR, NMR, TGA, HPLC	192
Exiguobacterium sibiricum DR11 *Exiguobacterium undae* DR14	PS	30 days	8% 8.8%	WL, FTIR, AFM	111
Consortium of *B. subtilis* MZA-75 and *P. aeruginosa* MZA-85	PS-PU	20 days	NM	WL, SEM, FT-IR, Sturm test (CO_2 evolution test)	193
Rhodococcus ruber C208	PS	8 weeks	0.80%	WL, SEM	194
B.cereus *B. gottheilii*	PS	40 days	7.4% 5.8%	SEM, WL, FTIR	108
P. aeruginosa DSM 50071	PS	60 days	NM	SEM, XRD, contact angle analysis, XPS, NMR, ATR-FTIR	96
B. paralicheniformis G1	PS	60 days	34%	FTIR, DSC, NMR, SEM	95
B. subtilis P. aeruginosa Staphylococcus aureus Streptococcus pyogenes	PS	1 month	20% 5% 4.762% 8.33%	WL	195
Xanthomonas sp. and *Sphingobacterium sp.*	PS	8 days	56%	WL	196
Microbacterium sp. NA23, *Paenibacillus urinalis* NA26, *Bacillus sp.* NB6, *P. aeruginosa* NB26	PS	8 weeks	NM	SEM, FTIR, HPLC	112
P. otitidis, *B.cereus*, and *Acanthopleurobacter pedis*	PVC	9 months	NM	FT-IR, SEM, GPC, DSC	82
Bacillus sp. AIIW2	PVC	3 months	0.26%	SEM, AFM, FTIR	197
P. citronellolis and *B. flexus*	PVC	30 days	19%	FTIR, GPC	198
B. gottheilii	PP	40 days	3.60%	SEM, WL, FTIR	108
Lysinibacillus sp.	PP	26 days	4%	WL, SEM, GC-MS, ATR-FTIR, XRD	117
P. aeruginosa WZH-4 *P. aeruginosa WGH-6*	PP	40 days	9.35% 17.2%	WL, SEM, FTIR, TGA, DSC	116

Table 1 Continued...

Strains	Plastic Type	Incubation time	Weight loss (WL) (%)	Techniques used	References
Heteroatomic backbone					
C-C backbone					
Ideonella sakaiensis 201-F6	PET	6 weeks	NM	NM	46
Pseudomonas sp. and *Bacillus* sp.	PET	8 weeks	3%	SEM, ATR-FTIR, NMR, WL	199
Brevibacillus parabrevis and *P. aeruginosa*	PET	90 days	NM	FE-SEM, GC-MS, XRD, ATR-FTIR	200
B. subtilis Staphylococcus aureus Streptococcus pyogenes	PET	1 month	74.59% 8.75% 3.846	WL	195
Clostridium thermocellum	PET	14 days	62%	WL, SEM	201
B.cereus B. gottheilii	PET	40 days	6.6% 3%	WL, SEM, FTIR	108
B. subtilis	PET	NM	NM	SEM, IR	47
Alcaligens faecalis	PET	10 weeks	15.25% and 21.72%	WL, FTIR, XRD, SEM, AFM	202
B. licheniformis	PET	1 month	NM	FTIR, SEM, Strums test	203
Pseudomonas sp. DBFIQ-P36	PU foams based on castor oil	2 months	30%	FTIR, INSTRON mechanical tester, SEM, GC-MS, NMR	204
P. protegens strain Pf-5	PU (Impranil DLN)	24h	NM	NM	70
Acinetobacter gerneri P7	PU (Impranil DLN)	NM	NM	SEM	69
B. amyloliquefaciens, M3	PU-PE	1 month	30–44 %	SEM, FT-IR, TGA, and XRD	73
B. subtilis JBE0016	PU	NM	NM	SEM, FTIR, GPC, GC–MS	68
Bacillus sp. AF8, *Pseudomonas sp.* AF9, *Micrococcus sp. AF10, Arthrobacter sp.* AF11 and *Corynebacterium sp.* AF12	PU	1 month	NM	SEM, FTIR, Sturm test	66
P. putida	PU	4 days	NM	FTIR	71
P. aeruginosa	PU -diol	10 days	32%	HPTLC, GC-MS	72

LDPE, low density polyethylene; HDPE, high density polyethylene; PE, polyethylene; PS, polystyrene; PVC, polyvinylchloride; PP, polypropylene; PET, polyethylene terephthalate; PU, polyurethane; NM, not mentioned; FTIR, Fourier transform infrared; SEM, scanning electronic microscopy; GC-MS, gas chromatography mass spectroscopy; AFM, atomic force microscopy; TGA, thermogravimetric analysis; HPLC, high performance liquid chromatography; NMR, nuclear magnetic resonance; XPS, X-ray photoelectron spectroscopy; XRD, X-ray diffraction; DSC, differential scanning calorimetry; GPC, gel permeation chromatography; HPTLC, high performance thin layer chromatography.

Due to the high complexity in the polymer structures of PU and the lack of in-depth research, an effective biodegradation at a promising rate has not yet been documented and the complete metabolic pathways of microbial PU degradation are still not sufficiently clear.[64]

PU degrading enzymes

Microbial degradation of PU is mainly mediated by the action of two classes of enzymes oxidoreductases and hydrolases, through oxidation or hydrolysis. The hydrolases involved include ureases attacking the urea bonds, proteases attacking the amide bonds, and esterases attacking the many ester bonds.[67]

It has been reported that a wide range of Gram-positive and Gram-negative bacteria release enzymes that can break down PU.[70] In which, Esterases (EC 3.1) are the main enzyme implicated in the hydrolysis of polyester-based PU. Indeed, they hydrolyze the ester bonds in the soft segments leading to the release of carboxylic acid and alcohol terminal groups.[67] Also, cutinases (EC 3.1.1.74) are involved in the degradation of PU, in which, they degrade some lipids and esters.[67] Proteases and amidases can intrinsically hydrolyze peptide or amide bonds and have been shown to hydrolyze urethane bonds in PU.[67] Moreover, Ureases (EC 3.5.1.5) hydrolyzes the urea bonds in poly(urea-urethane) polymers, releasing two amines and carbon dioxide. However, there are few reports on PU degradation by ureases, as the urea bonds are hard to be degraded compared to ester bonds.[67]

Several ester- and urethane hydrolases that degrade PU have been identified including PU esterases A (PueA) and B (PueB) from *P. protegens* Pf-5,[70] PU esterase PudA from *Comamonas acidovorans*, PU lipase (PulA) from *P. fluorescens*.[67] Also, *B. subtilis* MZA-75 employs both extracellular and cell associated esterases to utilize polyester PU as carbon source.[68]

In order to significantly lower the obstacles to the biocatalytic breakdown of PU in cooperation with the polyester hydrolases, future research should concentrate on the screening of enzymes having "polyurethanase" activity.[67]

Rafiemanzelat et al.[73] developed new poly (ether-urethane-urea) and tested their microbial degradation susceptibility with the

strain *B. amyloliquefaciens* isolated from Soil. Only few studies have reported the degradation of PE-PU.[64]

Degradation of plastics with C-C backbone

Polyvinyl chloride (PVC)

PVC mechanism biodegradation

PVC, a carbon backbone synthetic polymer that contains chlorine element, is the third highest produced plastic and is widely used in coating materials, electronics, medical devices, and food packing.[74–76] It is highly hydrophobic and highly stable covalent bond make PVC resistant towards biodegradation. Therefore, there is no efficient PVC-degrading bacterial have been reported.[75,77]

Some PVC are made with the addition of plasticizers as a result the growth of microorganisms on PVC film could be justified due to degradation of plasticizer.[29,78] A limited number of bacterial strains have been reported to degrade PVC polymer. *P. citronellolis* and *B. flexus,*[79] *P. putida* strain AJ and *Ochrobactrum* TD[80] were able to degrade PVC films containing additives. As well as *Klebsiella* sp. EMBL-1 is able to depolymerize and utilize PVC as sole energy source.[81] Although, a bacterial consortium capable of growing with PVC materials have been reported.[79,82]

The studies of PVC-degrading bacteria are limited (Table 1). Although, little is known about the bacterial degradation pathway and enzymes involved.[29] A recent study by Zhang et al.[81] has reported the degradation pathway of PVC by *Klebsiella* sp. EMBL-1 using a multiomic approach. They identify genes encoding enzymes involved in PVC degradation including genes potentially encoding dehalogenases such as non-heme chloroperoxidase and HAD family hydrolase genes which are reported for dechlorination activities of some halogenated compounds that could be involved in PVC dechlorination. Also, they propose that the catalase-peroxidase depolymerizes PVC polymer into lower-molecular weight polymers. Then the depolymerized PVC products would be transformed into shorter products through a series of enzymatic reactions possibly catalyzed by monooxygenase and dioxygenase which they might participate in oxygen addition to carbon chain, as above-mentioned for PE degradation.[81] The oxidation of polymer facilitates its contact with other extracellular enzymes such as lipase and esterase.

PVC degrading enzymes

A study by Zhang et al.[81] carried out a proteomic approach to identify the enzymes involved in PVC degradation including catalase-peroxidase which catalyze the polymer depolymerization, dehalogenases, enolase, aldehyde dehydrogenase, oxygenase, dihydroxy-acid dehydratase, which can potentially degrade depolymerized products through cleavage of carbon-oxygen bonds. Additionally, an entericidin EcnA/B family protein, which could be involved in the strain's stress responses to toxic substances a porin OmpC and other outer membrane proteins, which might transport some small-molecule metabolites and a glutamate synthase large subunit, which is involved in ammonia assimilation.

Polyethylene (PE)

PE mechanism biodegradation

Polyethylene (PE) is a major petroleum-based plastic that represent about 92% of synthetic plastics produced.[83] It is widely used in production of plastic bags, bottles, packaging materials.[5,23]

The most common PE is Low Density Polyethylene (LDPE) and High-Density Polyethylene (HDPE). They differ in their density, degree of branching and availability of functional groups on the surface.[5,83,84]

PE backbone chains contain only C–C bonds without hydrolysable groups, therefore PE is resistant to degradation.[83] Therefore, the initial step for PE degradation is the oxidation of PE polymer which leads to the formation of oxidized oligomers.[85] This step is initiated by insertion of hydroxyl groups in different positions into alkane chain: terminal and subterminal, and in middle chains under the action of alkane monooxygenases and/or hydroxylases.[5] In the terminal oxidation pathway, alkanes are first oxidized at their terminal carbon to produce the corresponding primary alcohols, then, under the action of alcohol dehydrogenase (Adh), in which oxidize hydroxy groups to carbonyl groups to produce the corresponding ketone which are further oxidized by aldehyde dehydrogenases to produce alkanoic acids. In subterminal oxidation, the corresponding alcohols produced after hydroxylation is oxidized to produce ketone. Followed by the formation of ester by a Baeyer-Villiger monooxygenase (BVMO) that insert oxygen atom adjacent to the carbonyl carbon. The ester is further hydrolyzed by esterase generating alcohol and fatty acid.[5,25]

PE degradation products, alkanoic acids and fatty acid, can further be used as metabolites and carbon sources (Figure 2).

Several bacteria were investigated to degrade different types of PE (Table 1). Among these bacteria belonging to the genera *Pseudomonas*, *Ralstonia, Stenotrophomonas*, *Klebsiella*, *Acinetobactor*, *Rhodococcus*, *Staphylococcus*, *Streptococcus*, *Streptomyces*, *Bacillus*, etc.[5,83,86] Two bacteria *B. amyloliquefaciens* (BSM-1) and *B. amyloliquefaciens* (BSM-2) were isolated from municipal solid soil and used for LDPE degradation.[87] Actinobacteria also have a high ability for PE biodegradation.[88] Additionally, *Pseudomanas* species have reported as effective strains in degrading PE such as *P. knackmussii* N1-2 and *P. aeruginosa* RD1-3.[89,90]

PE degrading enzyme

Studies have been reported the enzymes involved in PE degradation metabolism which include alkane monooxygenase, hydroxylases, laccases, peroxidases, alcohol dehydrogenase, aldehyde dehydrogenase, BaeyerVilliger monooxygenase, esterase, cutinase, and lipase.[91] These enzymes have been reported as enzymes related to PE degradation pathway in various bacteria. Alkane monooxygenase (AlkB) and hydroxylase was found to be important in the breaking down of PE.[83] In addition to AlkB, P450 enzymes could be part of the degradation machinery in PE-degrading bacteria. Yeom et al.[25] proposed a pathway for PE degradation in which PE polymer can be hydroxylated by a hypothetical hydroxylase (including cytochrome P450).

Zadjelovic et al.[91] have identify enzymes involved in alkane degradation such as two cytochrome P450, three alkane monooxygenases AlkB and two enzymes involved in the degradation of long-chain alkanes AlmA from the bacterium *Alcanivorax* sp. 24. PE biodegradation have also been reported using laccase.[85,92]

Polystyrene (PS)

PS mechanism biodegradation

PS is the fifth mostly used synthetic polymer[93,94] in packaging materials, food containers and construction materials.[95,96,97] PS is an aromatic thermoplastic with a C-C backbone,[81] makes its biodegradation very difficult.[81,98,99]

PS degradation can be performed via direct ring cleavage and side-chain oxygenation.[98] Depolymerization of PS generate different aromatic compounds that can further metabolized to be utilized as carbon sources (Figure 2).[100–102] In the first pathway, styrene is oxidized into styrene oxide by a styrene monooxygenase which further leads to the formation of phenylacetaldehyde under the action of styrene isomerase followed by the degradation of phenylacetaldehyde to acetyl-CoA.[28,103,104] Several bacterial were able to use this pathway for PS degradation such as *P. putida* CA-3.[105,106] Another proposed pathway is the direct ring cleavage, starts with the hydroxylation of styrene to produce styrene cis-glycol by styrene dioxygenase which then converted to 3-vinylcatechol by cis-Glycol dehydrogenase which further converted to acetyl-CoA by cis-glycol dehydrogenase.[29,103,107] Furthermore, the aromatic ring of PS can be degraded by aromatic ring hydroxylases or monooxygenases. However, degradation pathway and involved enzymes have not still been revealed.[81,97,98]

Styrene can be used by several bacterial genera, such as *Pseudomonas, Baccilus, Exiguobacterium* and *Rhodococcus*.[98] For instance, *B. cereus* and *B. gottheilii* have been elucidated for their PS degradation.[108] Additionally, a poly-extremophilic bacteria belonging to the genus *Exiguobacterium* have also demonstrated the ability to degrade PS.[100,109–111] Kim et al.[99] investigated the biodegradation of PS by mesophilic bacterial *P. lini* JNU01 and *Acinetobacter johnsonii* JNU01. Some bacteria such as *Microbacterium* sp. NA23, *Paenibacillus urinalis* NA26, *Bacillus* sp. NB6, and *P. aeruginosa* NB26 from soil have been studied for biodegradation of PS.[112]

PS degrading enzyme

The enzymatic mechanism is initiated by hydroxylation of PS in which is mostly catalyzed by cytochrome P4500s, alkane hydroxylases and monooxygenases.[28,98,106] For instance, alkane-1-monooxygenase (AlkB) was revealed to catalyze PS hydroxylation as a first step in PS degradation in *A. johnsonii* JNU01.[99] Also, Cytochrome P450 from *Bacillus subtilis* can catalyze the epoxidation of styrene.[113] Homoserine dehydrogenase (HDH) and S-formylglutathione hydrolase (SGT) were reported as target enzymes for PS biodegradation in *Pseudomonas* sp. DSM50071.[97] Alkane hydroxylases may degrade PS C-C bonds under acidic or alkaline conditions.[114] Studies suggest that styrene breakdown by bacterium *Exiguobacterium* sp RIT 594 occurs via two enzymes include an aromatic ring-cleaving dioxygenase and a hydrolase.[100] As mentioned in PET degrading enzymes, PETase catalyze the enzymatic degradation of PET. A recent study by Rocco et al.[115] reported a recombinant PETase that have an activity on both PS and PET.

Polypropylene (PP)

PP mechanism biodegradation

PP is the second widely used synthetic plastics and is frequently used in packaging.[32,116] This polymer has similar properties as PE; however, it is more resistant to biodegradation.[26,117]

To date, there are no detailed bacterial mechanism degradation of PP.[116,118,119] Nevertheless, some studies reported that pretreatment of PP might facilitate its biodegradation.[29,118,120] the pretreatment techniques include UV-irradiation, thermal and chemical treatment that helps in the decrease of polymer hydrophobicity and introduces groups such as carbonyl, carboxyl and ester functional groups, which made the polymer more susceptible to degradation.[26,121]

For instance, when PP is exposed to pyrolysis it produces aliphatic hydrocarbons that might follow the same pathway as PE degradation (Figure 2).[118,120] Aliphatic hydrocarbons can be oxidized to generate alcohol under the action of alkane hydroxylase, then alcohol can be converted to aldehyde by alcohol dehydrogenase, and aldehyde can be oxidized to fatty acid by aldehyde dehydrogenase. Fatty acids can be further metabolized through β-Oxidation to produce acetyl-CoA.[116,118,120] However, there are no PP-degrading enzymes have been reported yet.

Few studies of PP biodegradation have been reported (Table 1)[26,29,116] and the majority of this research used a pretreated PP.[26] *P. aeruginosa*, WZH-4 and WGH-6 were able to grow using PP as sole carbon source.[116] Additionally, it was found that *Bacillus* sp. strain 27 and *Rhodococcus* sp. strain 36, isolated from mangrove environments could also degrade PP.[122] Moreover, Wróbel et al.[123] found that seven bacterial strains (five *Serratia marcescens* and two *Enterobacter* spp.) could degrade PP. Also, *Lysinibacillus* sp. JJY0216 is able to degrade unpretreated PP.[117] A study by Aravinthan et al. investigated the ability of two different combinations of microorganisms to degrade physically pretreated PP.[124]

II. Bioconversion of synthetic plastic into polyhydroxyalkanoates (PHA)

Recent research points the way toward the search for sustainable development and the conversion of conventional plastic to bioplastics. Bioplastics are a sustainable alternative to petroleum-based plastics.[24,125] They significantly reduce the environmental impact of synthetic plastics, contributing towards bio-economy and a greener future.[1,126] In this regard, Polyhydroxyalkanoates (PHA) is the best alternative and sustainable to fossil-based plastics due to their high biodegradability in different environments, biocompatibility, thermoplasticity, chemical diversity, their production from renewable carbon resources, and release of non-polluting and non-toxic products after degradation.[127,128] PHA are a family of biodegradable polyesters, can be produced by a wide variety of microorganisms as intracellular carbon and energy reserves under various stress conditions.[129] According to their structural characteristics, PHA can be divided into two groups based on the number of carbon atoms: short-chain-length PHA (scl-PHA), which have 3–5 carbon atoms, and medium-chain-length PHA (mcl-PHA), which have 6–14 carbon atoms.[130] The most extensively studied type of PHA is PHB and the copolymer, Poly(3-hydroxybutyrate-co-3-hydroxyvalerate) P(3HB-co-3HV). Mcl-PHA have interesting mechanical properties, they are more flexible than scl-PHA and can be used in various applications.[131,132] Owning to their variable structure, PHA covers interesting properties from rigid brittle plastics to flexible plastics depending on the structure and composition of the polymer. PHA's versatile material characteristics allow their use in numerous sectors, essentially in plastics market.[133] Owing to their desirable characteristics, PHA have many applications including in biomedical sectors, agriculture, and packaging industries.[134,135] PHA are produced by pure and mixed microbial cultures or genetically modified strains using costly substrates, carbon sources represent 40–50% of total production cost.[136,137] High production costs of PHA in comparison to petrochemical plastics limits their commercialization.[138] The bioplastics market represents about 1% of the total global plastic produced.[1] Therefore, current researches are focused on optimization of cultivation conditions, selection of high-performing bacterial strains, and particularly the search of inexpensive feedstock for the achievement of higher PHA yield and lower production costs.[139] Since there are many wastes discarded in the environment and have harmful effects, recent studies focused on their use to produce PHA that helps in sustainable management of wastes and require a cost-effective process.[130] In this regard, numerous studies have demonstrated the production of PHA from organic waste such as waste cooking oil,[140,141]

whey,[142,143] waste water,[144,145] food waste,[146,147] which are a promising alternative for PHA manufacturing.[148,24] Plastic waste has also been used as carbon source for PHA production. Plastic-waste-based pyrolysis contains aliphatic and aromatic hydrocarbon compounds can be converted to PHA.[105,149,150] In recent years, conventional plastic biodegradation has become important in solving environmental plastic pollution. The monomers resulting can be further utilized by microorganisms and being converted into high value products such as PHA. PHA biosynthesis is performed via three well known and most described pathways, TCA cycle, fatty acid β-oxidation pathway, and fatty acid *de novo* biosynthesis pathway in which acetyl-CoA is the main precursor in PHA biosynthesis.[128,139] When sugars and fatty acids are used as substrate, they can be metabolized through *de novo* fatty acid biosynthesis or β-oxidation pathways producing scl-PHA. Indeed, PHA synthesis pathway consists of three reactions catalyzed through three specific enzymes. First step is the condensation of two acetyl-CoA under the action of β-ketothiolase to form acetoacetyl-CoA which further reduced (R)-3-hydroxybutyryl-CoA by acetoacetyl-CoA dehydrogenase. Then, PHB synthase polymerizes the (R)-3-hydroxybutyryl-CoA monomers into PHB.[151,152] Furthermore, fatty acids can be metabolized to (R)-3-hydroxyacyl-CoA by enoyl-CoA hydratase (PhaJ) through β-oxidation pathway or by transacylase (phaG) via *de novo* fatty acid pathway generating mcl-PHA.[153] Others pathways can be used for copolymers synthesis such as in PHBV synthesis, propionyl CoA is the precursor for the synthesis of 3-hydroxylvaleryl-CoA.[154,155] Moreover, synthetic plastics can be degraded via different metabolic pathways and used as substrate for PHA production (Figure 2).

1) Bioconversion of PET to PHA

Degradation of PET released different constituent monomers of EG, TPA, MHET and BHET by cleaving the ester bond.[29] Among these products, MHET could be further degraded into TPA and EG by the action of MHETase. Bioconversion of PET to PHA has been shown using di□erent bacteria.[156,157] *Ideonella sakaiensis* 201-F6 was the first reported bacterial strain capable to degrade and use PET as sole carbon source expressing two enzymes, PETase and MHETase, to hydrolyze PET and MHET into its monomers TPA and EG.[46] Afterwards, *I. sakaiensis* was investigated to accumulate PHA at high levels from PET.[158] A recent study by Tan et al.[159] explores *in vivo* and *in vitro* characterization of PHA synthase gene of *I. sakaiensis* ($phaC_{Is}$). Indeed, $phaC_{Is}$ was cloned and heterologously expressed in a PHA-negative mutant strain *Cupriavidus necator* PHB□4, the finding revealed that the strain produced P(3HB) accumulation of up to 71 wt% of the cell dry weight. Also, two co-cultivated engineered microbes could convert BHET to PHB. 5.16 g/L of BHET was hydrolyzed in 12 h, and 3.66 wt% PHB was accumulated in 54 h.[147] The strain *P. umsongensis* GO16 were isolated from soil.[156] Then, it was investigated for its potential use to developpe a process for the conversion of TA obtained from pyrolysis of PET into mcl-PHA.[157,160] Moreover, the engineered strain *P. putida* KT2440 was reported to convert EG to mcl-PHA.[161]

2) Bioconversion of PU to PHA

A wider range of breakdown products are produced by PU's complicated chemical structure, creating difficulties for downstream processing. Organic acids, organic alcohols, and diamines are the main biodegradation products of the complex structure of PU.[67]

In which, typical PU monomers released during the process of depolymerization are adipic acid (organic acids), 1,4-butanediol (organic alcohols), 2.4′ -Toluene Diamine (diamines) and ethylene glycol.[162] In which, 1, 4-butanediol (BDO) is oxidized to 4-hydroxybutyrate (4HB) which is the monomer of the short-chain-length PHA. Adipic acid (AA) is catalyzed by succinyl-CoA transferase to adipyl-CoA. Then, 2,3-dihydroadipyl-CoA is generated, which is then catalyzed to 3- hydroxyadipate-CoA under the action of 3-hydroxyacyl-CoA dehydrogenase. Succinyl-CoA and acetyl-CoA are formed under the acyl-CoA thiolase catalysis.[67] Then the Succinyl-CoA is converted to succinate semialdehyde (SSA) by SSA dehydrogenase. The SSA is reduced to 4HB by 4HB dehydrogenase.[163] 2.4′ - Toluene Diamine (TDA) is oxidized, decarboxylated, and deaminated to form 4-amino-catechol, which may be converted into 5-amino-2-hydroxyl muconic acid in the form of diol, and then degraded and transformed through a metabolic pathway similar to catechuic acid (reviewed by).[67] EG can be used as a substrate for the production of PHA and glyoxylic acid, which have a wide range of applications in the chemical industry.

Li et al.[63] reported that *P. putida* KT2440 is able to use 1,4-butanediol as a co substrate for the production of PHA and Ackermann et al.[164] found that this strain can convert AA into PHA by the expression of the *dcaAKIJP* genes encoding the adipyl-CoA transferase, dehydrogenase, and putative adipate uptake proteins from *Acinetobacter baylyi.* Another *Pseudomonas* species *P. capeferrum* can use a mixture of PU monomers including 2,4-TPA, AA, BDO, EG to produce PHA.[165]

3) Bioconversion of plastics with carbon back-bones into PHA

Depolymerization of PS generates different aromatic compounds. As mentioned above the degradation of styrene monomer might perform via two distinct pathways, the direct aromatic ring cleavage pathway and vinyl side-chain oxidation pathway generating acetyl-CoA. In which acetyl-CoA can be converted to PHA.[29,166] Ward et al.[105] reported that *P. putida* CA-3 convert styrene oil after pyrolysis to PHA as the sole carbon source. Styrene oil (1 g) was converted to 62.5 mg of PHA. *Cupriavidus necator* H16 is another bacterium that converts PS into PHA.[167] Furthermore, *P. putida* NBUS12 and *P. putida* S12 are reported to convert styrene to PHA.[168,169] Another study by Johnston et al.[167] carried out the potential use of predegraded PS for its bioconversion into PHA.

PE, PP and PVC have the similar carbon–carbon backbone chains. Pretreatment such as thermal treatment helps in this polymer biodegradation. Indeed, pyrolytic hydrocarbons can be degraded via oxidation process similar to microbial degradation pathway of n-alkane generating acetyl-CoA via β-oxidation as mentioned above which can be converted to PHA. It has been demonstrated that pretreated PP can serve as a carbon source for PHA production. For instance, *Cupriavidus necator* H1 have carried out to use oxidized PP solid waste to produce copolymers of 3-hydroxybutyrate and 3-hydroxyhexanoate (PHBH).[170]

P. aeruginosa PAO-1 has been shown to accumulate 25 % of the cell dry weight as PHA using pyrolytic hydrocarbons of PE in the presence of rhamnolipids.[171] Ekere et al.[172] reported the ability of *C. necator* to accumulate PHA copolymers (3-hydroxybutyrate, 3-hydroxyvalerate, and 3-hydroxyhexanoate) using PE from Tetra Pak waste packaging materials. Also, *Ralstonia eutropha* H16 was shown to accumulate PAH when supplied with non-oxygenated PE pyrolytic hydrocarbons as a carbon source.[33] Furthermore, *Ralstonia eutropha* H16 investigated for its ability to produce PHA using oxidized polyethylene wax (O-PEW) as carbon source. PHA produced contained 3-hydroxybutyrate, 3-hydroxyvalerate and 3-hydroxyhexanoate co-monomeric units.[173]

PVC, although pyrolysis has been shown to be able to depolymerize PVC into hydrocarbons. These products are of similar chemical compositions to those of PE and PP, which are able produce valuable chemicals. There are no reports about microbial strains that can utilize PVC pyrolysis products as carbon source so far.[29]

III. Evaluation methods for plastic biodegradation and characterization of byproducts

Biodegradation of plastics can be assessed with the changes of physical and chemical properties. The most used techniques are summarized (Table 1). Indeed, degradation efficiency of plastics polymer can be measured through various variables including weight loss (WL) by thermogravimetric analysis (TGA), carbon dioxide emission, changes of polymer surface topography using scanning electron microscopy (SEM) or atomic force microscopy (AFM) and X-ray diffraction (XRD), hydrophilicity or hydrophobicity of surface polymer using water contact angle analysis (WCA). Moreover, changes of chemical properties can be detected by FT-IR to evaluate the changes in functional groups and GC-MS to analyze and identify products generated by plastics biodegradation.[5,51,67,83,174,175] Characterization methods can only provide qualitative evidence.[67] However, these methods used such as changes in surface structure and weight loss for assessed plastics degradation might result from additives degradation. Therefore, it is important to find more efficient methods to evaluate the degradation of plastics.[83,176]

Conclusion

PHAs are biopolymers widely used in several industrial fields. Among the drawbacks on which researchers from all over the world are working is the reduction of production cost, the increase of biomass and PHA yields and the improvement of mechanical and thermal stability properties of these polyesters. Also, there is an urgent need to reduce the increasing pollution of the planet by synthetic plastics, which has become an unfortunate issue that requires a real reflection on effective solutions to face this challenge. This study illustrates and examines the main successful bioconversion pathways of petroleum-based plastics into biodegradable PHA materials. Nevertheless, there are still some challenges that require further research. One key issue is the need of a deeper understanding of the different pathways of plastic degradation to develop more advanced biotechnology techniques.

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Conflicts of interest

The authors declare that they have no competing interests

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