



Review

Sustainable polyhydroxyalkanoates in the bioeconomy: A review of recent advances in production innovations, economic feasibility, and patents landscape

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ABSTRACT

In light of the global environmental crisis caused by traditional plastics and their pollution, there is an urgent need for sustainable alternatives to plastics derived from fossil fuels. Polyhydroxyalkanoates (PHA) is a microbial intracellular energy reserve with the potential to replace petroleum-based plastics and reduce environmental pollution. PHA exhibits mechanical and thermal properties comparable to petroplastics, with the added advantages of biodegradability and biocompatibility. Furthermore, their physicochemical versatility makes them suitable for a wide range of applications, including eco-friendly packaging, agricultural mulch films, and innovative medical devices. However, large-scale PHA adoption remains constrained by production costs, as well as by challenges in scalability, feedstock supply, and downstream extraction, which all culminate in an uncompetitive minimum selling price (MSP) estimated at \$4–8/kg. Considering the aforementioned, this review aimed to provide a comprehensive evaluation of strategies for enhancing PHA production efficiency within a circular bioeconomy framework. It examines intrinsically diverse microbial communities that produce PHA, fermentation strategies, feedstock diversification, and green recovery techniques. It also evaluated emerging application trends and industrial potential, focusing on more than 20 PHA-related patents filed between 2020 and 2025. Finally, this study examined the economic feasibility of PHA production and identified feasible pathways toward more cost-competitive adoption of the biopolymer.

Abbreviations

PHA	Polyhydroxyalkanoate
MSP	Minimum selling price
3HB	3-hydroxybutyrate
3 HV	3-hydroxyvalerate
4HB	4-hydroxybutyrate
3HHx	3-hydroxyhexanoate
P(3HB)	Poly(3-hydroxybutyrate)
P(3 HV)	Poly(3-hydroxyvalerate)
P(3HB-co-3 HV)	Poly(3-hydroxybutyrate-co-3-hydroxyvalerate)
P(3HO)	Poly(3-hydroxyoctanoate)
CDW	Cell dry weight
NGIB	Next Generation Industrial Biotechnology
MMC	Mixed microbial consortia
VFAs	Volatile fatty acids
CSTRs	Continuous stirred-tank reactors

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iMBRs	Immersed membrane bioreactors
DMC	Dimethyl carbonate
DESS	Deep eutectic solvents
scCO ₂	Supercritical carbon dioxide
TEA	Techno-economic assessment

1. Introduction

Plastic pollution remains a defining environmental crisis, damaging oceans, harming wildlife, and endangering human health, primarily through microplastic contamination [1]. Globally, annual plastic production has exceeded 400 Mt./year and is projected to surpass 700 Mt. by 2040 [2,3]. Even under optimistic scenarios, global recycling

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capacity, estimated at only 150–200 Mt./year, is far below production rates, resulting in continued waste accumulation [2]. Without systemic interventions encompassing sustainable design, production decarbonization, and the integration of a circular bioeconomy, plastic pollution and its associated greenhouse gas emissions are expected to intensify further [3]. In response to this challenge, the concept of a circular economy has gained global prominence. It is an economic system designed to eliminate waste and pollution, keep products and materials in use, and regenerate natural systems [4]. Unlike the traditional “take–make–dispose” linear model of production, this resource-efficient strategy aims to extend material life cycles and retain resources within the economic system for as long as possible [3]. Building on these principles, the circular bioeconomy applies circularity to biologically based value chains, emphasising renewable feedstocks, waste valorisation, biodegradability, and closed-loop material flows [5,6]. Within this framework, the production of Polyhydroxyalkanoates (PHA) from renewable feedstocks as sustainable replacements for conventional plastics exemplifies the integration of biotechnology, green chemistry, and circular manufacturing in the pursuit of a circular bioeconomy [5,6]. As such, PHA polymers stand out among emerging bioplastics for their dual environmental and functional advantages. PHAs combine complete biodegradability with physicochemical versatility, enabling their use as substitutes for conventional petrochemical plastics across diverse applications.

PHA polymers are intracellular carbon and energy storage materials naturally synthesised by over 300 microbial species, including bacteria, archaea, and photoautotrophs [7]. Their accumulation typically occurs under conditions of excess carbon sources but limited nutrients, such as nitrogen, phosphorus, magnesium, or oxygen [7]. While nutrient limitation is a common trigger for PHA production, it is not universal; some naturally occurring and engineered strains, notably marine purple non-sulphur bacteria [8] and certain cyanobacteria [9], can produce PHA even during growth phases. The classical biosynthetic pathway for PHA involves three key enzymes: 3-ketothiolase (PhaA), acetoacetyl-CoA reductase (PhaB), and PHA synthase (PhaC), which convert acetyl-CoA into poly(3-hydroxybutyrate), the simplest short-chain-length PHA (SCL-PHA) [10]. Alternative pathways, including β -oxidation and fatty acid de novo synthesis, expand the monomer pool to medium- and long-chain-length PHA (MCL- and LCL-PHA) with varying physicochemical properties [10]. At the core, PHA comprise repeating hydroxyalkanoate monomers containing hydroxyl (–OH) and carboxyl (–COOH) groups linked by ester bonds (Fig. 1) [11]. The main PHA monomers include 3-hydroxybutyrate (3HB), 3-hydroxyvalerate (3HV), 4-hydroxybutyrate (4HB), and 3-hydroxyhexanoate (3HHx) [12]. They are broadly classified based on chain length into SCL-PHA (3–5 carbon

atoms), MCL-PHA (6–14 carbon atoms), and long-chain-length PHA (LCL-PHA; > 14 carbon atoms) [7]. Poly(3-hydroxybutyrate) (P(3HB)), poly(3-hydroxyvalerate) (P(3HV)), and their copolymer, poly(3-hydroxybutyrate-co-3-hydroxyvalerate) (P(3HB-co-3HV)), are highly crystalline thermoplastics suitable for rigid applications [13]. MCL-PHA, poly(3-hydroxyoctanoate) (P(3HO)) and poly(3-hydroxynonanoate) (P(3HN)) exhibit elastomeric, latex-like properties [14]. LCL-PHA (e.g., poly(3-hydroxypentadecanoate) and poly(3-hydroxyhexadecanoate), though less common, provide enhanced flexibility due to longer side chains [15].

Despite their biodegradability and versatility, PHA remain three to five times more expensive than petrochemical plastics due to costly feedstocks, energy-intensive recovery, and low productivity [16]. Recent advances, however, are narrowing this gap. Robust and engineered strains (e.g., via CRISPR/Cas9) have improved yields [17], extremophiles such as *Haloflex mediterranei* enable non-sterile fermentations [18], and waste-derived feedstocks align production with the circular-bioeconomy [19]. Additionally, green extraction methods now achieve >90 % recovery with reduced environmental impact [20].

Over the past three decades, PHA has been reviewed from many angles, including recent studies on scale-up [21], recycling [22], and advanced genetic strategies for production [17], among others. Although these studies are valuable, a holistic perspective remains scattered across multiple sources. Therefore, this review consolidates recent advances into a unified narrative, recognising that industrial viability depends on tackling high production costs through the dual lens of biological and process innovation. The biological dimension encompasses metabolic and genetic modifications, exploitation of extremophiles, mixed microbial consortia, and photoautotrophic platforms. The process dimension covers renewable feedstock utilisation, non-sterile fermentation, and eco-friendly polymer recovery. Finally, the review examines the broadening scope of PHA industrial applications, including recent patents, addresses the economic feasibility of PHA production, and outlines future directions critical for scaling up cost-effective PHA production. This article is expected to facilitate the transition from niche bioplastics to mainstream carbon-neutral materials.

1.1. Literature and patent search strategy

The literature for this review was identified through systematic searches in Scopus, Web of Science, PubMed, and ScienceDirect databases. Search strings included: (polyhydroxyalkanoates OR PHA) AND (engineered strains OR mixed cultures OR thermophilic fermentation OR algal bioplastics) AND (renewable feedstocks OR non-sterile fermentation OR green extraction) AND (techno-economic analysis OR biodegradation OR PHA applications). Inclusion criteria were based on topic relevance, publication type, recency, language (English), and the presence of experimental or validated data. Exclusion criteria included irrelevant or duplicate studies, non-peer-reviewed sources, and outdated publications. Over 80 % of the cited works were published from 2020 onwards. Patent data from 2020 to 2025 was obtained via Google Patents, covering filings indexed from major international intellectual property offices. The patent analysis focused only on innovations in PHA product applications.

2. Biological innovations for sustainable PHA production

The choice of microbial platform is a foundational decision that dictates the process design, feedstock compatibility, and economic feasibility in PHA production. At the heart of these efforts are two interdependent dimensions: modifying metabolic pathways to expand substrate utilisation and monomer diversity and using genetic engineering tools for precise genome editing. Beyond classical biosynthetic routes, engineered and alternative pathways, notably non- β -oxidation pathways and CO₂ fixation, are unlocking more sustainable and

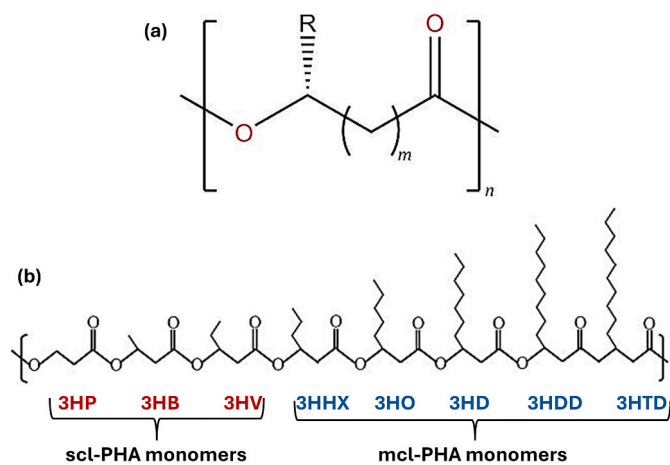


Fig. 1. (a) General molecular formula of PHA (R = alkyl group or side chain, m = 1–8, and n = 100 to 1000) (b) commonly synthesised short-chain-length PHA monomers (SCL-PHA) and medium-chain-length PHA monomers (MCL-PHA).

potentially carbon-neutral PHA production [23,24]. Direct sugar-to-PHA conversion via non- β -oxidation pathways streamlines metabolic flux, reduces cellular energy demands, and enables the incorporation of high-value monomers such as 3HHx [23]. Likewise, autotrophic CO₂-fixation in *Cupriavidus necator* and cyanobacteria integrates in situ carbon capture into the production cycle [24]. Alternative MCL- PHA pathways, including glyoxylate shunt engineering, further diversify polymer structures [25], complemented by PhaC synthase modifications that expand substrate tolerance, enabling the incorporation of novel monomers such as 3HHx [26]. Alongside these engineered strains, extremophiles capable of thriving in harsh, low-energy conditions, resilient mixed microbial consortia on variable, low-cost substrates, and photoautotrophic systems are emerging as frontier platforms for industrial-scale manufacture using a broad spectrum of feedstocks (Table 1).

2.1. PHA production by metabolically and genetically engineered organisms

Genetic and metabolic engineering offer powerful tools for designing “ideal” production strains with enhanced yields, tailored polymer compositions, and the ability to utilise low-cost feedstocks, ultimately reducing production costs. Early strategies focused on overexpressing

the core PHA biosynthetic enzymes PhaA (3-ketothiolase), PhaB (acetoacetyl-CoA reductase), and PhaC (PHA synthase) to funnel excess acetyl-CoA into PHA granules [27]. Recently, the advent of synthetic biology tools such as CRISPR–Cas9 and λ -Red recombineering has enabled markerless genome editing, targeted gene deletions, and entirely novel pathway assembly, drastically reduced unintended mutations and enabled rapid chassis optimisation across diverse bacteria [17,28]. In *Halomonas bluephagenesis* TD01, a seamless CRISPR/Cas9 system achieved 100 % efficient deletion of the *prpC* gene, which encodes 2-methylcitrate synthase in the propionate degradation pathway, and increased the 3-HV fraction in P(3HB-co-3 HV) by 16-fold relative to the wild strain [29]. *Pseudomonas putida* KT2440, which is normally unable to metabolise ferulic acid, produced 270 mg/L PHA after the integration of nine heterologous genes using the CRISPR/Cas9n- λ -Red system [25]. Recently, coupling the deletion of a stress-response/biogenesis gene with lipase engineering in *Cupriavidus necator* H16+ elevated PHA productivity by 25.4 %, yielding 264 g/L polymer from palm oil substrates, one of the highest reported volumetric outputs in this organism [30]. Similarly, the halotolerant *Halomonas bluephagenesis* was engineered to co-produce 3HB, 4HB, and 3 HV monomers directly from glucose by chromosomal integration of 4HB and 3 HV pathway genes and deletion of the *lpxM* gene, which encodes myristoyltransferase involved in outer membrane biogenesis. This modification enabled

Table 1
Overview of PHA production by advanced microbial systems.

Microorganism	Strain	Carbon source	PHA type	PHA (%)	Reference
Extremophiles	<i>Aeribacillus pallidus</i> BK1,	Glucose	P(3HB)	77.15	[38]
	<i>Gordonia terrae</i> S-LD	Used soybean oil (USO)	P(3HB)	66.97	[57]
	<i>Halomonas alkalicola</i> Ext.	Galactose	P(3HB-co-3 HV)	45.57	[58]
	<i>H. boliviensis</i> DSM 15516	Industrial residues of the red algae (<i>Gelidium corneum</i>)	P(3HB)	41	[59]
	<i>H. mediterranei</i>	Dairy co-products	P(3HB-co-3 HV)	27.1	[60]
	<i>Halomonas</i> sp. YLGW01	High-fructose corn syrup (HFCS)	P(3HB)	67.39	[61]
	<i>H. taeanensis</i> YLGW01	Crude glycerol	P(3HB)	60	[62]
	<i>Salinivibrio</i> sp. M318	Waste fish oil and glycerol	P(3HB)	51.5	[63]
	<i>Caldimonas thermodepolymerans</i> DSM 15344	Xylose	P(3HB)	87.36	[64]
Recombinant	<i>Cupriavidus necator</i> PHB – 4	Fructose + δ -valerolactone + bean oil	P(3HB-co-3HHx-co-5 HV)	74.24	[65]
	<i>C. necator</i>	Fat/protein-emulsion	P(3HB-co-20.0 % 3HHx)	71	[66]
	<i>Halomonas bluephagenesis</i>	Glucose and 1,4-butanediol	P(3HB-co-14 mol% 4HB)	86	[67]
	<i>Haloferax mediterranei</i>	Glucose	P(3HB-co-3 HV)	NR***	[68]
	<i>Pseudomonas putida</i> KT2440	Sucrose	P(3HB)	38.1	[69]
	<i>Salinivibrio</i> sp. TGB10	Glucose + propionate	P(3HB-co-3 HV)	NR	[70]
	<i>Synechococcus</i> sp. PCC 7002 (KB15)	Photoautotrophic + acetate	P(3HB)	23.8	[71]
Mixed microbial consortia	<i>Bacillus</i> sp. SM01 and <i>C. necator</i> NCIMB 11599	Glucose and xylose	P(3HB-co-3 HV)	62	[72]
	Mixed microbial cultures	Highly saline pickle brine	SCL-PHA	74	[73]
	Mixed microbial cultures	Cheese whey wastewater	P(3HB)	24.5	[74]
	Mixed cultures from reground pasta effluent	Organic acids from the acidogenic fermentation of pasta waste	P(3HB)/HV/HHx	NR	[75]
	Mixed microbial cultures from municipal sludge	Synthetic VFAs; agri-food residue fermentate	P(3HB-co-3 HV)	20–30	[76]
	Mixed microbial consortia	Palm oil and derived wastewater	3HB/3 HV/3HO	30.5	[77]
	Purple phototrophic bacteria mixed cultures	Butyric acid; carbohydrates	P(3HB)	20–29	[78]
	Waste-activated sludge	Methane + valeric acid	P(3HB-co-3 HV)	27 $\pm$ 3	[79]
Microalgae	<i>Chlorella sorokiniana</i> SVMIICT8	Sodium acetate	P(3HB)	29.5	[80]
	<i>Chlorella</i> sp.	Sunlight +0.2 % sodium bicarbonate	P(3HB)	80	[81]
	<i>Chlorella vulgaris</i>	BG-11 medium + NaNO ₃ + sodium acetate	P(3HB)	20	[82]
	<i>Desmodesmus communis</i>	Glucose and sodium acetate	P(3HB)	50	[83]
Cyanobacteria	<i>Arthrospira platensis</i>	BG-11 medium + NaNO ₃ + sodium acetate	P(3HB)	16.2	[82]
	<i>Nostoc muscorum</i>	Glycerol	P(HB-co-HV)	31.3	[84]
	<i>Synechocystis</i> sp.	Acetate	P(3HB)	31	[85]

*** NR- Not reported.

high-density growth and terpolymer accumulation, achieving 73 g/L cell dry weight (CDW) with 78 % terpolymer content in a 100 L unsterile fermenter [31]. A fed-batch cultivation on lignocellulosic hydrolysate enabled engineered *H. bluephagenesis* T39 to accumulate 42 g/L P(3HB) in a 7 L bioreactor, substantially higher than what is typically achieved by wild strains under similar conditions [32]. All of these illustrate the potential of synthetic biology to drive high-yield PHA production even under non-sterile, open-system conditions. However, such gains often come at a cost. Overexpression of synthetic pathways imposes a metabolic burden, diverting resources from growth and reducing cell fitness. As evident in the study by Favoino, et al. [33], *Pseudomonas putida* with multiple gene deletions showed slower growth despite higher P(3HB) yields. This underscores the trade-off between remarkable polymer yield, metabolic burden, and instability of the host strain.

Genetically engineered photosynthetic microorganisms also demonstrated direct fixation of CO₂ into P(3HB) via photoautotrophy [34]. In the works of Fink, et al. [35], a filamentous N₂-fixing cyanobacterium, *Nostoc* sp. PCC 7120 was engineered by expressing the *C. necator* P_{psbA}-phaC1AB operon together with the phasin gene phaP1, resulting in significant accumulation of P(3HB) without nitrogen starvation or compromising cell viability. However, low efficiency of photosynthesis, high photobioreactor costs, and limited light penetration make this approach economically impractical. Metabolically and genetically engineered microbes have achieved notable gains in PHA titers, monomer specificity, and substrate flexibility [30,31]. Despite these advancements, challenges such as metabolic burden, genetic instability, and inconsistent performance on complex feedstocks constrain industrial scalability [33,39]. The path forward lies in integrating strain engineering with optimised bioprocesses and sustainable feedstocks, ensuring that genetic gains translate into robust, economically viable PHA production at scale.

2.2. PHA production by extremophiles

Extremophiles, particularly halophiles and thermophiles, offer a practical route to reducing two major operational costs during PHA production, viz., sterilisation and contamination. The abilities of halophiles to thrive in high-salt conditions and thermophiles to thrive in high-temperature conditions eliminate the need for sterilisation and promote continuous open fermentation, thereby improving operational simplicity and reducing costs [36]. Halophiles, such as *Halomonas*, can use inexpensive feedstocks, non-sterile seawater, minimising freshwater use and energy costs for steam sterilisation. For example, *Halomonas nigricans* X339 achieved 5.11 g/L of P(3HB) from unsterilized wheat straw hydrolysate in open-batch fermentation at 2 % salinity and pH 9.0, demonstrating both high substrate conversion (0.30 g P(3HB) per g of substrate) and industrial feasibility [19]. Although high substrate conversion reflects efficient carbon utilisation, it does not always translate into high volumetric productivity, which depends on the rate of polymer accumulation over time. Moreover, high-salinity systems may require investment in corrosion-resistant reactors and specialised downstream equipment, which can offset a portion of the operational savings.

Thermophiles exhibit a remarkable but highly variable capacity for PHA accumulation, with yields significantly influenced by the cultivation temperature and substrate. For instance, *Bacillus thermoamylovorans* strain PHA005 produced 50.77 % PHA on sodium octanoate, and optimisation raised the yield to 63.27 % at 45 °C [27]. Likewise, *Caldimonas thermodepolymerans* grown on xylose at 50 °C achieved 80 % PHA in its CDW [37]. Notably, *Aeribacillus pallidus* BK1 demonstrated markedly elevated PHA yields under short-term thermal shocks, increasing from 35.63 % at 60 °C to 75.46 % at 90 °C [38]. Although thermophiles are advantageous for lignocellulosic integration, they may introduce complexities in process control. For instance, although *C. thermodepolymerans* accumulates high PHA content, it actively degrades extracellular PHA at elevated temperatures, indicating a dynamic balance between synthesis and degradation that may complicate the

maximisation of yields [37]. Collectively, extremophiles embody the principles of Next Generation Industrial Biotechnology (NGIB), which emphasises robust, genetically engineered cell factories capable of unsterile, continuous, and modular bioprocessing [39]. By integrating systems biology with process intensification, NGIB aims to align microbial resilience with circular bioeconomy goals [39].

2.3. PHA production by mixed microbial consortia

Mixed microbial consortia (MMC) are gaining traction for their cost-effectiveness and eco-friendliness. Unlike pure cultures, MMC leverages the interactions among diverse microbial species to utilise multiple waste streams efficiently, reducing production costs and environmental impact [40]. Functional specialisation within the community enhances versatility, as different taxa hydrolyse complex substrates, convert intermediates into volatile fatty acids (VFAs), and accumulate PHA, collectively improving productivity [41]. MMC systems demonstrated intracellular PHA contents exceeding 50 % and yields above 0.5 g/L, valorising waste and reducing costs relative to a pure culture system. For example, activated sludge enrichments from wastewater treatment plants achieved PHA contents of 22.1 ± 1.5 g PHA/g volatile suspended solids (VSS) during rapid accumulation cycles [42]. More recently, odd-chain VFAs (propionic and valeric acids) valorisation by MMC yielded up to 616.47 mg /L P(3HB-co-3 HV) under optimised feast-famine conditions [43]. Likewise, sequential feast-famine methanotrophic processes converted methane and VFAs into 0.5 g/L of P(3HB-co-3 HV) [44]. These findings underscore the operational resilience of MMCs to fluctuating and heterogeneous substrates, eliminating the need for costly refined feedstocks. However, there are concerns about product consistency, which may result from fluctuations in monomer composition in response to changes in feedstock and community dynamics, thus limiting applications that require precise polymer specifications [45]. Interestingly, systematic assembly of microbial consortia to target precise substrate utilisation and PHA synthesis has been noted to enhance compositional control as well as polymer yield. For instance, Amabile, et al. [46] showed that synthetic co-cultures of *Methylocystis parvus* and *Rhodococcus opacus* efficiently produced PHA copolymer from waste-derived VFAs, achieving up to 73.7 % polymer content. Their findings revealed that valeric acid and VFAs enhanced P(3HB-co-3 HV) accumulation, particularly in the presence of methane [46]. Similarly, food-waste hydrolysate reactors, dominated by *Meganema*, *Thauera*, and *Paracoccus*, reached biomass densities of 13.9 g/L and achieved PHA titers of 12.7 g/L over 80 days [47]. Furthermore, maintaining stable community structures over extended operation is challenging; recent meta-omics studies demonstrated that viral contamination and phage-bacterial dynamics can disrupt dominance patterns within the consortium [45,48]. In all, these findings highlight the need for real-time monitoring and advanced process control to stabilise community function and ensure reproducible polymer quality.

2.4. PHA production by microalgae and cyanobacteria

Recent advancements have demonstrated the potential of microalgae and cyanobacteria for sustainable PHA production compared to that typically produced by bacteria [49,50]. These photoautotrophic organisms offer several advantages, including rapid growth rates, high biomass productivity, and the ability to capture carbon dioxide (CO₂), thereby mitigating greenhouse gas emissions [51]. They can also be cultivated in open ponds or simple photobioreactors, significantly reducing the high energy and capital costs associated with sterile fermentation typical of bacterial systems. Historically, the first cyanobacterial P(3HB) producer, *Chlorogloea fritschii*, reported in 1966, accumulated approximately 10 % P(3HB) /CDW under photoautotrophic conditions [52]. More recently, *Chlorella vulgaris* cultivated in a wastewater-fed bioreactor simultaneously produced 20 mg/L PHA and sequestered all free CO₂ within three days [53]. These examples

highlight the environmental promise of algal systems, but economic and operational feasibility remain major constraints. Compared with heterotrophic bacteria, which routinely achieve >80 % PHA of CDW and titres exceeding 100 g/L, these photosynthetic systems show much lower accumulation. For example, 4.18 % PHA in CDW was reported for *Arthrospira platensis* [49] and more recently, 11 % by *Chlorogloeopsis fritschii* in 20 % whey [54]. Consequently, the final product yield is typically in the milligrams-per-litre (mg/L) range, far below levels required for economically viable bulk production. Downstream processing also presents challenges; for instance, variability in algal biomass and rigid algal cell walls complicates extraction, necessitating integrated, solvent-minimized purification strategies to preserve polymer quality [55,56]. Despite these shortcomings, the most immediate potential of microalgae and cyanobacteria PHA production lies in niche, high-value applications (e.g., biomedicine, speciality packaging) where environmental credentials can offset low volumetric productivity. Ultimately, scalability will depend on coupling carbon capture benefits with techno-economic innovations that make these systems competitive within the circular bioeconomy.

3. Process innovations for sustainable PHA production

As surmised earlier, microbial innovation is central to broadening the scope of PHA production. However, the long-term viability of the bioplastic industry hinges on innovative strategies addressing economic, environmental, and technical barriers to scale-up. These innovations include diversifying feedstocks through the valorisation of agro-industrial and municipal wastes, implementing non-sterile fermentation systems to reduce energy and costs, and developing innovative downstream recovery methods that minimise harmful solvent use and environmental toxicity (Fig. 2).

3.1. Feedstock diversification and waste valorisation

Similar to most microbial-based bioprocesses, the choice of carbon feedstock has a significant impact on the economics and sustainability of

PHA bioproduction. Generally, feedstock costs account for ~50 % of overall process costs and directly influence the environmental footprint through land use and upstream inputs [86]. Typically, first-generation feedstocks, primarily sugar- and starch-rich crops such as sugarcane, corn, and sugar beets, are used because of their high fermentable carbohydrate content [87]. These edible feedstocks have enabled robust PHA yields exceeding 60 %/CDW [86]. However, diverting food crops to material production raises ethical concerns about food security and exerts significant environmental pressure for the intensive use of land, water, and agrochemicals [88]. To circumvent this, focus is progressively shifting to second-generation feedstocks that leverage lignocellulosic biomass (LCB), agro-industrial residues, municipal waste streams, and non-edible oils [89,90]. The conversion of LCB to fermentable sugars requires pretreatment methods to break down the recalcitrant structure and make cellulose and hemicellulose accessible, such as steam explosion, acid hydrolysis, alkaline pretreatment, and biological pretreatment [91]. In recent studies, LCB, such as sorghum stover [92], wheat straw [19], rice straw [93], and oil palm empty fruit bunch [94], have been utilised for microbial PHA production, thereby mitigating reliance on arable land and food crops. This approach not only avoids competition with food crops but also valorises agricultural residues. However, feedstock variability and the presence of inhibitors may necessitate the use of robust microbial strains and process control to ensure consistent PHA yield and productivity. Industrial by-products, such as whey permeate and cheese whey from dairy processing, have also been shown to support economically viable PHA production. *Hydrogenophaga pseudoflava* DSM1034 produced 0.144 g/g of P(3HB) per sugar consumed when cultivated in whey permeate [95]. *Haloferax mediterranei* demonstrated even greater versatility, accumulating 9.1 mg/g/h of P(3HB-co-8 %3 HV) from hydrolyzed whey without addition of 3 HV precursors [96]. Likewise, when cultivated on cheese whey-derived VFAs, *H. mediterranei* achieved 2.43 g/L of P(3HB-co-3 HV) [18].

In the same vein, significant potential has also been recorded with third-generation feedstocks, which primarily include algae and other non-traditional carbon sources, such as methane and carbon dioxide

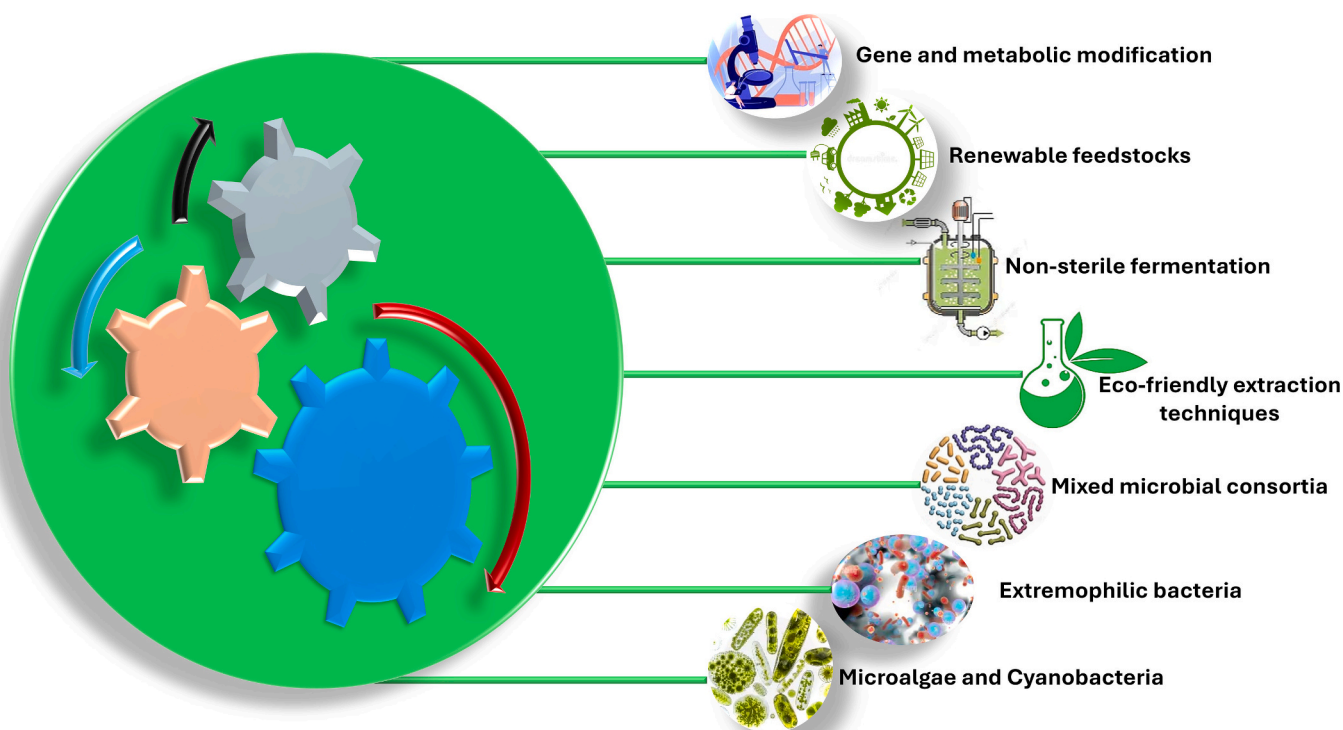


Fig. 2. Integrated cost-reduction strategies for sustainable PHA production.

[97]. Microalgae and cyanobacteria capture atmospheric CO₂ and convert it into carbohydrates and lipids, which can subsequently be hydrolysed or fermented directly by bacteria to produce PHA [98]. Recent studies have demonstrated the feasibility of using algal hydrolysates for PHA production. *Cupriavidus necator* (DSMZ 545) produced 73 g of P(3HB-co-3 HV) using glucose derived from *Chlorella vulgaris* starch and levulinic acid in fed-batch fermentation [99]. Likewise, *Priestia megaterium* produces 7.5 g/L of PHA with cellular contents as high as 75 % from *Chlorella* sp. biomass hydrolysate [100]. *Halomonas* sp. YLGW01 accumulated 2.6 g/L of P(3HB) from red seaweed (*Eucheuma spinosum*) hydrolysates, which increased to 3.9 g/L after detoxification [101]. Beyond microalgae, significant progress has been made in exploiting methanotrophic bacteria for the direct conversion of methane gas (CH₄) into PHA. Methane-oxidising bacteria such as *Methylosinus trichosporium* OB3b [102], *Methylocystis suffitae* [103], *Methylocystis* sp. [104], *Methylobacterium* sp. [105], and *Methylosinus* sp. [106] have demonstrated the ability to produce PHA from methane. In a recent study, *Methylocystis*-dominated activated sludge achieved 95.8 % CH₄ conversion into 36 % P(3HB) and a biomass of 0.59 g/g CH₄ [107]. This offers an innovative route for greenhouse gas mitigation while simultaneously generating value-added bioplastics. The evolution from food crops to residues and novel carbon sources reflects the PHA industry's dynamic progression toward sustainability. Realising full industrialisation will require continued investment in pretreatment technologies, microbial engineering, and process integration, ensuring that diverse feedstocks can be harnessed reliably and economically within a circular bioeconomy framework.

3.2. Non-sterile fermentation method for PHA production

Complementing feedstock diversification, innovations in fermentation design, particularly non-sterile systems, offer significant opportunities to lower energy inputs and simplify operations. Traditional fermentation processes require strict aseptic conditions to prevent contaminating microbes that compete with PHA-producing strains or degrade the product, thereby increasing capital and operating costs, thereby negatively impacting scaling up. By eliminating sterilisation, non-sterile fermentation reduces costs, energy use, and process complexity, positioning it as a transformative approach for sustainable PHA production [108]. However, optimal bioreactor design and operation are central to the success of non-sterile systems. The tuning of operational modes and parameters has been noted to influence selective microbial enrichment and stability of PHA accumulation [21]. In stirred-tank systems, for instance, the key is to impose selective pressures, such as salinity, feast–famine cycles, or nutrient limitation, which suppress contaminants while favouring PHA-accumulators [109]. Continuous stirred-tank reactors (CSTRs), whether single or staged, enable functional separation: upstream units impose short feast phases to enrich productive microbes, while downstream reactors maintain famine conditions to maximise polymer accumulation [110]. Careful tuning of dilution rates and oxygen transfer allows staged CSTRs to consistently enrich PHA-storing microbes under open conditions, offering a scalable framework for non-sterile processing [111].

In practice, sequencing-batch operation remains the workhorse for open processes because its cyclic feast–famine design naturally enriches storage strategists [112]. Recent studies have demonstrated that cycle architecture, including feast duration, aeration regimes, and decanting strategies, directly governs stability and polymer yields under non-sterile conditions [113]. Furthermore, biomass retention technologies are increasingly integrated with non-sterile fermentation to stabilise productive microbial communities [109]. Immersed membrane bioreactors (IMBRs) decouple hydraulic and biomass residence times, permitting continuous effluent removal while retaining productive cells [114]. This configuration stabilises microbial communities under fluctuating waste-derived substrates, sustaining high yield in long-term, semi-continuous cultivation [114]. Other reactor designs have also

shown potential. Notable among these is the airlift system, which facilitates high oxygen transfer, lower shear stress, and reduced fouling compared to impeller-driven tanks [115]. Internal-loop airlifts have been applied for P(3HB) production by *Stenotrophomonas rhizophila*, where gas-flow control created oxygen transfer profiles conducive to selective enrichment under open conditions [116]. For phototrophic PHA production, open thin-layer, tubular, and capillary photobioreactors maximise light capture and CO₂ utilisation while minimising contamination through design-driven selectivity [117].

Across all reactor types, control strategies are as critical as geometry. Online monitoring of off-gas composition, redox potential, and dissolved oxygen enables dynamic adjustment of feeding regimes and identification of feast–famine transitions. In continuous and plug-flow-like designs, internal recirculation sharpens substrate gradients, reinforcing spatial selection while maintaining throughput [112]. Increasingly, open PHA systems are integrated with waste-to-VFA pretreatment units, requiring reactors that buffer fluctuating feedstocks and tolerate inhibitors. Hybrid configurations, such as staged CSTRs or SBRs coupled with IMBRs, are emerging as robust solutions that combine ecological selection pressures with engineering stability [118]. A study demonstrated effective PHA production using a three-reactor system: one anaerobic reactor for VFAs generation, followed by two aerobic reactors for microbial enrichment and P(3HB) synthesis [119].

Despite these advantages, technical challenges remain. High salinity complicates downstream recovery, as salts reduce extraction efficiency and necessitate tailored purification strategies such as membrane separation or compatible solvent systems [120]. Scale-up studies further indicate that maintaining stable extremophilic populations requires precise control of pH, ionic strength, and oxygen transfer; fluctuations can lead to contamination or reduced yields [121]. Contamination management is therefore critical. Recent studies highlight the use of robust or engineered microorganisms capable of outcompeting invaders [122]. Selective antimicrobial agents, including bifunctional compounds like piperazine, have been used to simultaneously nourish target organisms and inhibit contaminants [123]. In summary, non-sterile fermentation offers clear advantages over conventional aseptic systems by reducing sterilisation costs and enabling greater flexibility in substrate use. However, these gains are balanced by challenges in contamination control, polymer consistency, inhibitor tolerance, and scale-up. The most promising path forward lies in hybrid strategies that integrate ecological selection (e.g., feast–famine enrichment) with engineering solutions (e.g., biomass retention, online monitoring, modular reactor design). Continued advances in reactor engineering, microbial robustness, and contamination management will be essential to translate laboratory successes into industrially scalable, cost-competitive processes.

3.3. Innovations in extraction techniques

As the final downstream process in the PHA value chain, extraction plays a decisive role in determining both the environmental footprint and economic viability of production. PHA extraction requires cell wall disruption (chemical, mechanical, or biological), followed by selective extraction to achieve high purity (>95 %) while preserving polymer integrity [124,125]. The classical approach employs halogenated organic solvents, such as chloroform [126] and dichloromethane [127], to dissolve PHA. While these solvents yield high-purity polymers, they pose serious environmental, health, and safety hazards [128]. The following subsections discuss recent innovations in greener, sustainable alternative extraction techniques (Fig. 3).

3.3.1. Green-solvent extraction

Among recovery strategies, solvent extraction remains the most established. Green solvents focus on biodegradability, low toxicity, and recyclability, which are crucial for aligning PHA recovery with circular bioeconomy goals. Early proof-of-concept for green solvent extraction

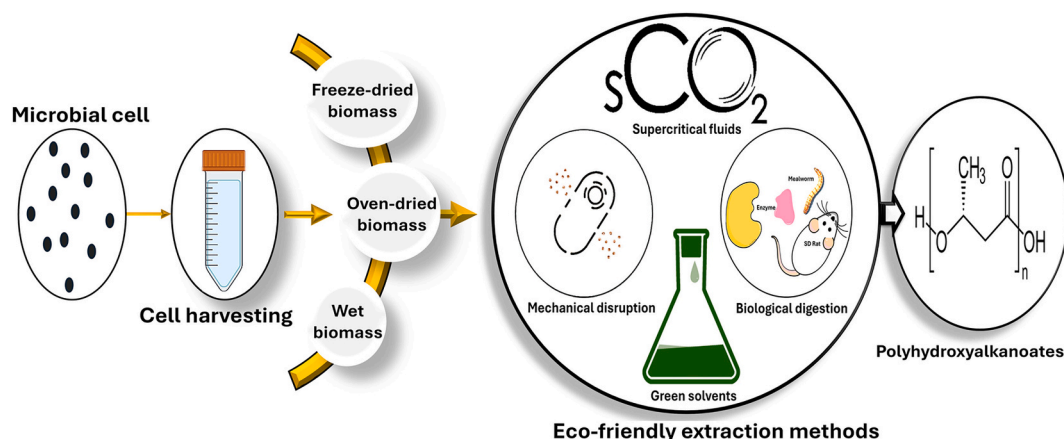


Fig. 3. Eco-friendly PHA extraction techniques from wet, dried, or lyophilised cells.

came with the introduction of dimethyl carbonate (DMC), a fully biodegradable solvent as an alternative to chlorinated solvents. DMC achieved 85–95 % recovery and 98 % purity from *Cupriavidus necator* [129] and MMC [130] with no molecular weight loss, which is critical for downstream applications and regulatory safety, especially in food packaging. Likewise, a recent study further highlighted its ease of recycling and scalability, reporting 83.3 % recovery of P(3HB) (75 % purity) from *Chlorogloea fritschii* [131]. Although the use of DMC aligns with toxic waste reduction goals, achieving high purity often requires a secondary purification step, like an ethanol wash, which adds to the process cost and complexity [132]. Ethyl acetate, a renewable, low-toxicity ester which is generally regarded as safe (GRAS) with a favourable boiling point (77 °C), achieved >90 % PHA recovery with 93–97 % purity, making it suitable for a range of PHA copolymers, including P(3HB) and P(3HB-co-3 HV) [133,134]. More recently, Didion, et al. [135] reported 95 % yield and 97 % purity of P(3HB) extracted from *Pseudomonas putida*, underscoring ethyl acetate's versatility across diverse PHA types. Acetone, another acceptable solvent in food processing and extraction, has also shown potential for selective extraction of MCL-PHA, which exhibits lower crystallinity and greater solubility than SCL-PHA. For instance, acetone was used to selectively extract MCL-PHA from *Pseudomonas umsongensis* GO16 without solubilising P(3HB), confirming its suitability for targeted MCL-PHA recovery [136]. Likewise, acetone was identified as one of the most effective solvents for the recovery of P(3HB-co-3 HV) from MMC, achieving 95 % yield and 96 % purity [137]. In contrast, acetone generally acts as an anti-solvent for SCL-PHA due to its high crystallinity and low solubility [138]. However, under pressurised, elevated-temperature conditions, rapid recovery with yields and purities comparable to those of chloroform (96.8 % and 98.4 %, respectively) was achieved, with the added benefit of near-complete solvent recovery [138]. Despite these advantages, acetone's volatility and flammability demand strict safety measures during scale-up operations. Recently, deep eutectic solvents (DESs), especially hydrophobic natural DESs such as thymol:vanillin and thymol:decanoic acid mixtures, have emerged as innovative extractants offering the combined advantages of sustainability and efficacy. Reports of >90 % polymer purity at moderate recovery yields (42–85 %) from mixed-culture biomass indicate their potential for integrated biorefinery processes with lower environmental impact [139,140]. DESs show promise for integration into biorefinery systems, though their recyclability and regulatory safety remain ongoing challenges, especially for food-contact applications. From a sustainability perspective, green solvents provide an effective balance between performance and environmental safety, reducing toxic waste and enabling solvent recovery. Yet, challenges with solvent loss and process costs limit their scalability. This makes solvent-free approaches such as supercritical fluid extraction or mechanical disruption more attractive

for large-volume, lower-value markets where cost efficiency outweighs slight reductions in purity.

3.3.2. Supercritical fluid extraction

To overcome solvent-related toxicity and recovery costs, supercritical fluid extraction has emerged as a clean, solvent-free alternative. This technique exploits the dual gas–liquid nature of supercritical fluids, particularly supercritical carbon dioxide (scCO₂), which, above 74 bar and 31 °C, can penetrate microbial cells and dissolve PHA without leaving toxic residues [11,141]. To improve polymer–solvent interactions, small polar cosolvents such as methanol or ethanol are often introduced as modifiers [142]. Recent studies have highlighted that modifiers, when combined with biomass pretreatments, significantly enhance extraction efficiency. For instance, Haghighi, et al. [142] achieved up to 97.3 % recovery and 97.2 % purity from mixed microbial cultures using scCO₂ at 20 MPa, 35–40 °C, with methanol as a modifier. Likewise, Nayır, et al. [143] achieved 80 % P(3HB) recovery from activated sludge using scCO₂ at 200 bar and 40 °C with methanol as a modifier. Despite the upfront investment in high-pressure equipment, scCO₂ extraction stands out for its minimal solvent residue, low energy consumption for solvent evaporation, and potential for CO₂ recycling within closed systems. It thus aligns strongly with clean-label, low-impact manufacturing initiatives. Compared to green-solvent extraction, scCO₂ avoids solvent loss and downstream purification steps, but its elevated equipment cost and limited throughput restrict its economic viability for bulk, low-value markets. In such cases, it is believed that mechanically driven methods are more accessible, whereas scCO₂ is best positioned for speciality applications where premium product quality justifies higher capital expenditure.

3.3.3. Mechanical disruption

Mechanically driven cell lysis techniques, such as high-pressure homogenization, sonication, and bead milling, eliminate the use of toxic chemicals and are suitable for large-scale operations [144]. High-pressure homogenization applies intense pressure to the microbial suspension, rupturing cells and releasing PHA, followed by centrifugation. This method has been demonstrated to achieve yields of nearly 100 % with purities exceeding 95 % for both P(3HB) and P(3HB-co-3HHx) [145]. Sonication utilises ultrasonic waves to generate cavitation-induced shear, thereby disrupting cell walls. When sonication and lysis buffer were combined, a PHA yield of 45 % was achieved [146]. Likewise, a 60 % yield of poly(3-hydroxyoctanoate) (P(3HO)) was achieved from *Pseudomonas putida* U through sonication [147]. On the other hand, bead milling uses glass beads to grind cells in a high-speed mill [146]. For instance, vortexing *Bacillus* sp. biomass with 5 g of glass beads for 15 min in lysis buffer yielded 35 % PHA, while grinding without buffer gave 34 % [144]. Despite their effectiveness and

environmental advantages, they are highly energy-intensive and require sophisticated equipment. A further drawback is the risk of polymer chain scission, which lowers molecular weight and compromises film-forming capacity and mechanical integrity [148]. Integration with mild solvent extraction or enzymatic pretreatment can ameliorate these drawbacks, preserving polymer properties critical for applications requiring stringent physicochemical specifications [149]. Compared to solvent-based methods, mechanically driven extraction avoids chemical hazards and solvent residues. However, its high energy demand and potential polymer degradation limit its competitiveness for high-value markets, where solvent-based or biological methods may offer superior product quality.

3.3.4. Biological recovery

Biological extraction methods employ enzymatic treatments and living organisms, such as mealworms and rats, to digest non-PHA cell components, thereby selectively preserving the biopolymer [150]. This method operates under mild conditions, reducing the risk of polymer degradation and contamination, as well as environmental concerns associated with the other methods. Hydrolytic enzymes such as lysozymes, proteases, nucleases, bromelain, and trypsin break down cell walls and intracellular materials, ensuring minimal damage to PHA granules [151]. For instance, *Streptomyces albus* Tia1, a non-PHA producer, secretes a proteolytic, caseinolytic enzyme that efficiently extracts PHA from *Priestia megaterium* Ti3 [152]. When coupled with green solvents such as 1,3-dioxolane, enzymatic pretreatment increased P(3HB) recovery to 94.5 % while reducing energy input compared to mechanical disruption [153]. However, the high cost of enzymes and the need for precise control over reaction conditions limit their industrial application [151]. Remarkably, the larvae of the mealworm beetle (*Tenebrio molitor*) have been explored as a biological method for recovering PHA. Mealworms have been shown to consume freeze-dried cells of *Cupriavidus necator* H16 and excrete the PHA granules in their faeces with comparable purity to chloroform-extracted PHA [154]. After the mealworms consumed the PHA-producing bacterial cells, the excreted PHA granules can be collected and further purified using water, detergents, and heat treatment to achieve almost 100 % pure PHA granules [154–156]. Likewise, Sprague-Dawley rats were fed *C. necator* H16 freeze-dried cells, and faecal material was collected and processed to obtain high-purity PHA granules [157]. Despite their environmental advantages, biological methods face significant barriers, including high enzyme costs, slow throughput, and stringent process control requirements, which limit their industrial adoption [151]. Consequently, biological recovery may be best suited to niche or small-scale applications where biodegradability, solvent-free processing, and polymer integrity are prioritised over cost. Biological recovery may be further potentiated by their applications in hybrid systems, where enzymatic pretreatment or biological digestion is combined with chemical or mechanical steps to balance purity, cost, and sustainability.

4. Economic and sustainability considerations in PHA production

The long-term sustainability of PHA production is considered as important as its economic feasibility; hence, the need to fulfil the three interdependent sustainability pillars of environmental performance, economic viability, and operational robustness [158]. In this regard, a truly sustainable PHA process must minimise carbon and toxicity footprints, use energy and solvents efficiently, and maintain stable productivity under variable feedstock conditions. While microbial platforms and other bioprocess innovations may address some of these criteria, their real-world impact depends on how effectively they are integrated into a cohesive production system [53]. Despite significant technological progress, PHA remain economically uncompetitive. The minimum selling price (MSP) typically ranges from \$ 4 to \$8/kg, compared to approximately \$1/kg for conventional plastics like polyethylene and

polypropylene [16]. This disparity reflects the combined effects of expensive feedstocks, relatively low process efficiencies, and energy-intensive downstream recovery. Bridging this gap requires integrated strategies that simultaneously address feedstock cost, process efficiency, and energy use guided by techno-economic assessment (TEA) to identify the most impactful cost levers. A central consideration for cost reduction lies in the valorisation of waste streams such as agro-industrial residues, food waste, and wastewater organics to provide a cheap carbon source for PHA production while contributing to waste management and circularity [77,159,160]. Although these feedstocks can potentially lower production costs by up to 50 %, their compositional variability and presence of inhibitory compounds often complicate process control, creating a trade-off between lower material costs and higher operational complexity [161]. To mitigate these challenges, robust microbial platforms such as genetically improved strains, extremophiles, MMCs, and photoautotrophic organisms, capable of maintaining stable productivity under non-sterile, nutrient-limited, or saline conditions, have been explored [35,57,113].

Recent TEA have demonstrated that integrating PHA production into biorefineries is an efficient pathway to sustainability; by coupling PHA synthesis with other value-generating processes, it can offset production costs and improve resource utilisation. For example, Shahzad, et al. [158] showed that coupling PHA production with the recovery of biodiesel and meat-and-bone meal co-products significantly enhances economic feasibility. Similarly, Rajendran and Han [162] simulated a biorefinery converting food waste into multiple products, including PHA, biohydrogen, ethanol, and 2,3-butanediol, to project a PHA minimum selling price (MSP) of \$4.83/kg, which could be reduced to \$2.41/kg by optimisation. Similarly, modelling of a halophilic PHA production system using cheese by-products showed a breakeven price under \$4/kg, with enzyme reuse and spent medium recycling enhancing efficiency and driving down substrate costs and consequently operating expenditure [163]. More recently, Khatun, et al. [159] simulated a modular system processing 450 t/day of food waste, reporting an MSP of \$3.67/kg. Collectively, these studies demonstrate that waste-integrated biorefineries and solvent recycling are among the most effective strategies for lowering MSP. Optimised systems approach \$2.5–3.5/kg, a threshold that begins to challenge conventional plastics when coupled with policy incentives. Across all these models, three parameters, substrate yield, fermentation performance, and downstream recovery, consistently emerge as the dominant determinants of overall economics. Specifically, downstream processing remains a major cost contributor, accounting for 40–60 % of total operating costs [162]. Green extraction methods, such as the use of DMC, ethyl acetate, DES, and scCO₂, offer lower toxicity and easier solvent recycling while maintaining recovery efficiencies comparable to those of halogenated solvents [130,140,143]. However, while DMC and ethyl acetate are flammable, DES are often viscous, and scCO₂ requires high-pressure equipment, thus limiting scalability. Mechanical disruption and enzymatic digestion avoid solvent residues but can be energy- or enzyme-intensive and may reduce polymer purity [145,153]. Thus, solvent selection and process design must balance environmental performance with economic feasibility within an integrated framework.

Ultimately, achieving sustainable and economically competitive PHA production requires a holistic balance between process innovation and system resilience. Waste-derived substrates reduce carbon footprints but introduce feedstock variability, demanding robust process control. Likewise, non-sterile and halophilic fermentations reduce energy and water consumption but may compromise product consistency and require robust strains and corrosion-resistant equipment. Green extraction techniques minimise environmental impacts yet often raise capital or operating costs [164]. Overcoming these trade-offs requires a unified process framework that combines renewable energy inputs, continuous fermentation, and efficient separation technologies, establishing a production model that is both circular and scalable [164]. Hence, overcoming the economic bottlenecks that currently impede PHA feasibility (Fig. 4) and achieving MSPs below \$3/kg will require

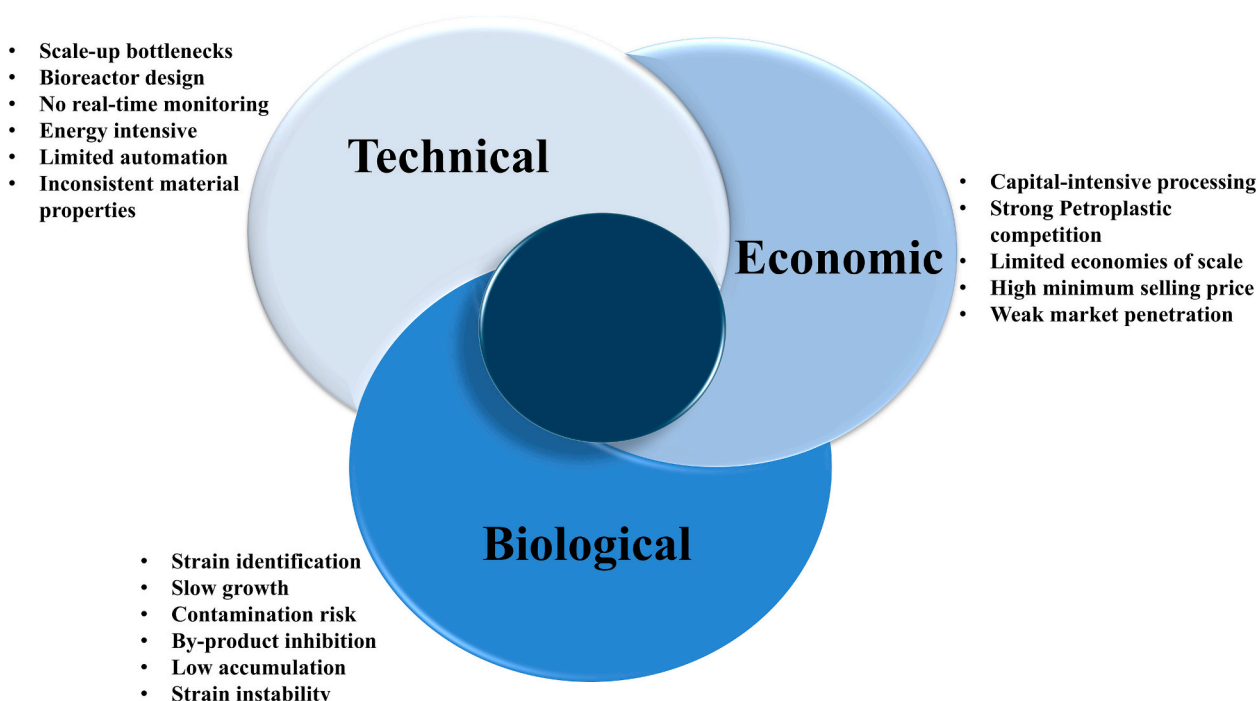


Fig. 4. Technoeconomic and biological constraints in sustainable PHA production.

systemic innovation rather than isolated process improvements. Bio-refinery integration that links PHA production with waste valorisation, nutrient recovery, and co-product generation offers the most promising pathways forward [6]. When coupled with technical innovations like

genetically engineered robust strains, continuous fermentation systems, and decentralised modular plants, cost competitiveness can be significantly enhanced. Finally, combining these integrated models with supportive policy instruments and carbon credit mechanisms is essential to

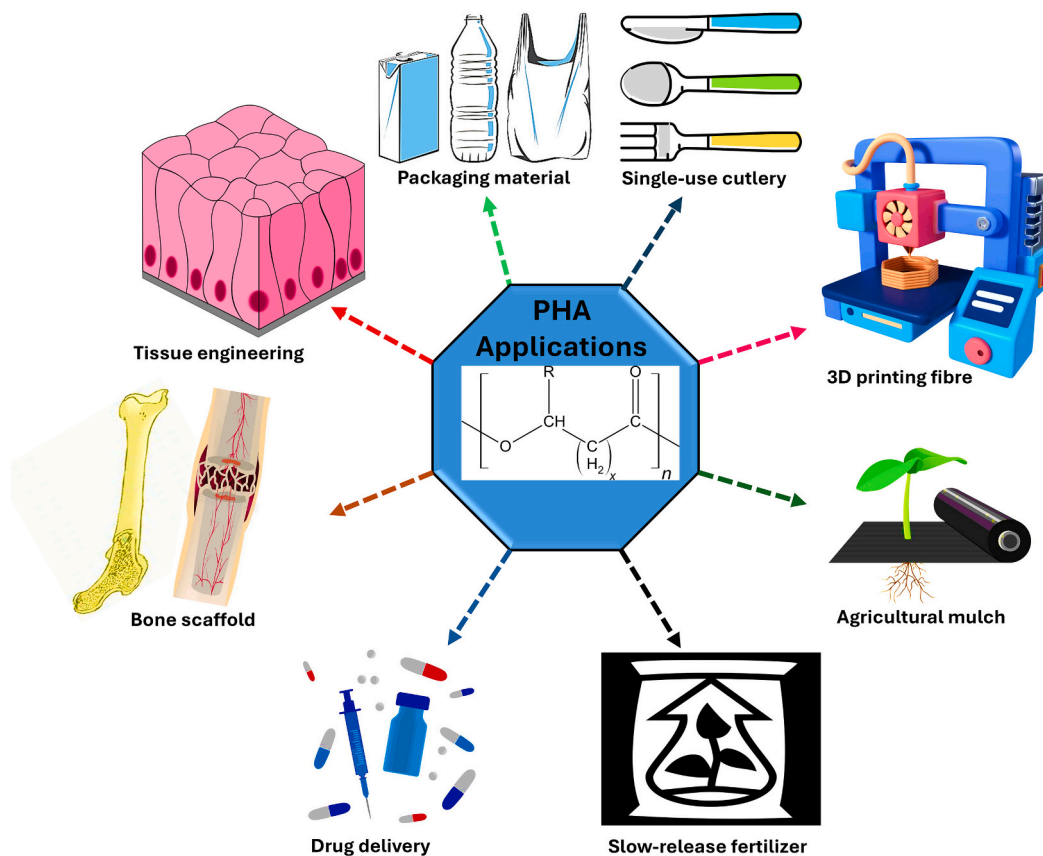


Fig. 5. Applications of PHA in diverse industries.

transition PHA from a niche bioplastic to a cornerstone of the circular bioeconomy [12,161].

5. Industrial applications of PHA

The application of PHA spans a wide range of industries, including medical, agricultural, and industrial sectors, as its biodegradability, biocompatibility, and versatility make it an attractive alternative to conventional plastics, promoting resource efficiency and minimising environmental impact. Single-use cutlery, packaging materials, textile materials, 3D fibres, medical implants, suture thread, slow-release fertiliser and pest control, and many more materials can be produced from PHA as shown in Fig. 5.

5.1. Medical application

PHA has found numerous uses in the medical industries due to its biocompatibility, biodegradability, and piezoelectric properties [165], especially in drug delivery systems [166] and tissue engineering [167]. PHA have been noted to support cell growth and elicit limited immune responses [168]; furthermore, their degradation products (3-hydroxy acids) are non-toxic and are readily metabolised [169]. PHA has been instrumental in the development of biodegradable implants for orthopaedic and surgical use, such as screws, plates, and pins, which degrade naturally in the body over time, eliminating the need for invasive surgery to remove the implant [170,171]. P(3HB-co-3 HV) has also been used in the fabrication of sutures that degrade in the body, reducing infection risk by providing wound support during the healing phase as well as excessive scarring [172]. Due to its porous structure and ability to support cell attachment and proliferation, PHA has been utilised to create scaffolds for bone, cartilage, and soft tissue regeneration [173]. In drug delivery, PHA has been engineered into nanoparticles or micro-particles to encapsulate therapeutic agents, providing controlled release and enhancing drug bioavailability [174]. Sha'at, et al. [166] formulated PHA nanoparticles encapsulating curcumin, achieving >75 % drug loading with pH-responsive release and excellent hemocompatibility. Similar advances have been reported in the development of biodegradable stents, which provide temporary vascular support and then degrade, reducing complications associated with permanent metal stents [175]. The study by Kalaoglu-Altan, et al. [176] showed that PHA stimulates the expression of human beta-defensin 2 and cytokeratin in HaCaT cells, supporting their suitability as wound dressing materials. In dentistry, PHA is used as a biodegradable membrane for guided periodontal regeneration, enhancing outcomes by removing the need for secondary membrane retrieval [177,178]. Additional applications include antimicrobial coatings for medical devices and carriers for imaging agents to improve diagnostic accuracy [179]. Despite these advances, several challenges remain. Ensuring consistent *in vivo* degradation profiles and maintaining mechanical integrity during the healing process are critical hurdles [180]. Furthermore, the production of medical-grade PHA at scale is constrained by high costs and the need to minimise batch-to-batch variability. Broader clinical adoption will depend on advances in copolymer design for tailored degradation, improved process control for medical-grade consistency, and regulatory harmonisation.

5.2. Agricultural applications

The utilisation of PHA in agriculture is primarily as biodegradable mulch films, addressing issues of disposability and persistence associated with traditional plastic films. PHA mulch films can be ploughed into the soil after use, degrading naturally and enriching the soil with organic matter, thus enhancing soil fertility and structure. For example, biodegradable mulches based on plasticised PLA/P(3HB) were reported to positively affect sweet pepper production and biodegrade completely within a month [181]. Additionally, PHA can be used to produce

biodegradable agricultural nets and grow bags, which support plants, provide shade, and protect crops from pests and harsh weather [182]. PHA polymers are also used in slow-release fertiliser systems, herbicides, and fungicides to achieve prolonged effectiveness. Fertiliser pellets coated with P(3HB) released 20 % of the ammonium nitrate, improving nutrient efficiency and reducing leaching losses [183,184]. Similarly, herbicides such as metribuzin and tribenuron-methyl encapsulated in P(3HB) or P(3HB-co-3 HV) microparticles exhibited strong activity against invasive weeds like Vietnamese balm [185]. Similarly, PHA-based seed coatings have been demonstrated to protect seeds from pests and diseases, enhance planting processes, and support seedling development [186]. As these biodegradable coatings break down, they release beneficial additives into the soil in a controlled manner, further reducing dependence on synthetic chemicals [187]. PHA polymers tailored for water retention and nutrient release may also improve crop yield, aligning with sustainable, circular agricultural cycles. PHA applications are also expanding into aquaculture. Recent studies highlight the use of PHA and its oligomers as immunostimulants and delivery systems that enhance disease resistance, stress tolerance, and gut health in farmed fish and shrimp, offering a biodegradable and non-toxic alternative to antibiotics and synthetic feed additives [188]. However, challenges persist in achieving price competitiveness and matching the mechanical durability of traditional films, which may be addressed through targeted copolymer production for enhanced toughness and multilayer film architectures that combine PHA with other biodegradable polymers to achieve performance comparable to traditional films.

5.3. Other notable applications of PHA

PHA polymers have become a promising solution for single-use items such as packaging materials and disposable cutlery, helping reduce plastic waste while meeting the growing consumer demand for sustainable products [168]. For instance, P(3HB-co-3 HV) films were shown to be suitable for food-contact applications due to their remarkable mechanical properties and water-vapour permeability for up to 10 days [189]. Likewise, P(3HB-co-3 HV)-based packaging material functionalized with tannins exhibited enhanced antioxidant, UV protection, and gas barrier properties [190]. PHA is also gaining traction in 3D printing due to their printability and environmental benefits in producing a wide range of products, from prototypes to functional parts, while ensuring eco-friendly disposal [191]. However, to improve PHA filament properties, they are often mixed with other polymers or natural fibres for 3D printing [192]. Duan and Wang [193] used selective laser sintering to fabricate 3D nanocomposite scaffolds of osteoconductive calcium-phosphate nanoparticles and P(3HB-co-3 HV), yielding porous constructs which demonstrated suitability for bone tissue engineering and clinical application. In the textile industry, PHA can be spun into fibres, just like nylon, to produce nonwoven fabrics for products such as medical masks, gowns, and sanitary items. Their biodegradability ensures that these fabrics do not persist in the environment after disposal, thereby tackling waste management challenges [194]. For example, single-jersey knitted fabrics from a novel bio-based, degradable PLA/P(3HB-co-3 HV) multifilament yarn were shown to possess thermo-mechanical properties that meet industrial requirements [195]. Looking ahead, potential uses for polyhydroxyalkanoates (PHA) in electronics include transient devices and flexible biocircuits that safely dissolve after use. These applications are particularly promising for medical diagnostics and environmental sensing. Additionally, space missions could explore producing PHA from their generated waste to manufacture tools and bioplastics during long-duration flights. These possible applications highlight the material's versatility, positioning PHA as a critical contributor to circular design and carbon-neutral innovation across various sectors.

6. Patent landscape of PHA

Patents related to PHA provide a unique window into the continuous industrial innovations and capture technological advances that are often not yet reported in academic literature. Thus, delving into the patent landscape of PHA offers valuable insights into the directions of industrial research, the strategies of leading companies, and the emerging trends that shape its global use. In this regard, a focused patent review was conducted to capture the most recent developments and commercial successes in PHA applicability, drawing on records from the Canadian Intellectual Property Office, the China National Intellectual Property Administration, the European Patent Office, the French National Institute of Industrial Property, the Japan Patent Office, the Spanish Patent and Trademark Office, and the United States Patent and Trademark Office. The search identified a substantial portfolio of patents on PHA applications as summarised in Table 2. The initial patent search revealed that thousands of PHA-related patents have been registered over the past four decades, encompassing industrial applications, production methods, processing, and polymer modification, among others. However, in this review, all this information was streamlined to the recent patent information on PHA application between 2020 and 2025. These patents underscore the accelerating industrial momentum of PHA across diverse application domains, including medical devices, biodegradable packaging, agricultural films, cosmetic formulations, 3D-printing materials, flame-retardant composites, and advanced functional materials such as piezoelectric devices and antimicrobial films (Table). Notably, most of these patents are assigned to industrial entities rather than academic institutions, reflecting substantial corporate investment in PHA-based product pipelines. This recent patent activity highlights not only the breadth of PHA's industrial integration but also the strategic positioning of companies to leverage PHA's biodegradability, biocompatibility, and functional tunability in high-value markets.

7. End-of-life scenarios for PHA

The sustainability of polyhydroxyalkanoates (PHA) extends far beyond their production phase to their end-of-life (EOL) pathways, where their inherent biodegradability distinguishes them from the persistent legacy of petroleum-based plastics. PHA are designed to reintegrate into natural carbon cycles through microbial degradation while also supporting recovery options such as mechanical and chemical recycling [222]. Understanding these EOL pathways is crucial for positioning PHA within the circular bioeconomy framework and ensuring that its use contributes meaningfully to global sustainability goals. Biodegradation is the most defining and advantageous EOL pathway for PHA, but it is neither uniform nor instantaneous. The degradation process depends strongly on polymer composition, whether SCL-PHA with high crystallinity, or MCL-PHA, which are more amorphous but hydrophobic [13,14]. Typically, SCL-PHA degrade via surface erosion because their crystalline domains limit enzyme accessibility, whereas MCL-PHA undergo bulk erosion at slower rates [12]. This process begins with extracellular depolymerases secreted by bacteria and fungi, which hydrolyse ester bonds in the polymer backbone, releasing water-soluble 3-hydroxyacid monomers [12,223]. These monomers are subsequently bioassimilated and mineralised to CO₂ and water under aerobic conditions, or to CO₂ and methane under anaerobic conditions [223,224]. Genera such as *Pseudomonas*, *Cupriavidus*, *Bacillus*, and *Actinomyces*, as well as fungi including *Ascomycota* and *Basidiomycetes*, have been shown to play pivotal roles in PHA degradation [37,224,225]. Nevertheless, it is important to emphasise that all currently commercialised PHA types, irrespective of their monomer composition, are biodegradable according to validated international standards EN 13432, ASTM D6400, and ISO 14855 across freshwater, marine, and soil environments [12]. This standardised biodegradability ensures that PHA polymers, despite structural variability, consistently meet global environmental performance criteria and are recognised as fully compostable under certified

conditions.

Controlled composting systems represent the most advanced application of PHA biodegradation, forming the basis of certification schemes such as EN 13432 and ASTM D6400, which require ≥90 % mineralisation within 180 days, along with disintegration and ecotoxicity criteria [226,227]. Industrial composting facilities operating at 55–60 °C with thermophilic consortia enable rapid conversion of P(3HB) and P(3HB-co-3 HV), often exceeding 95 % mineralisation within less than three months [228]. Home composting, however, is slower and more variable, with complete degradation typically requiring 6–18 months, though blending PHA with starch or other biodegradable polymers can accelerate disintegration [229]. Outside engineered composting environments, soil degradation occurs over 3–12 months, typically reaching 50–90 % conversion depending on moisture, pH, and microbial diversity [230]. Marine environments pose the greatest challenge, where mineralisation can extend over 6–24 months and is often mediated by sulphate-reducing bacteria in sediments [231].

While microbial activity is central, abiotic processes contribute by preconditioning PHA for biodegradation. Ultraviolet radiation induces photooxidation, triggering chain scission through radical-mediated Norrish reactions that lead to embrittlement and oligomer formation [232]. Thermal degradation, commonly observed during processing, involves random chain scission above 180 °C with crotonic acid as a key byproduct [233]. Mechanical abrasion can fragment PHA into smaller particles, increasing surface area for microbial degradation [234]. These abiotic pathways facilitate fragmentation and increase surface area for microbial attack but also raise emerging concerns. Laboratory studies have shown that PHA particles around 200 nm in size have the potential to have a long-term effect on aquatic organisms, even at concentrations as low as 110–50 mg/L [235]. Likewise, a recent study on *Mytilus edulis* shows reduced key antioxidant enzyme activities in gills and digestive glands after 96 h exposure to P(3HB) microplastics, indicating oxidative stress [236]. Although ultimately biodegradable, these transient intermediates underline the importance of evaluating PHA's environmental interactions across different scales.

Anaerobic digestion and landfilling represent other realistic EOL routes. In anaerobic digesters, PHA can be converted into biogas rich in methane, which can be captured for energy, along with a nutrient-rich digestate suitable for soil amendment [237]. In landfill conditions, mineralisation is slower, ranging from 20 to 50 % over 1–5 years, but facilities equipped with methane recovery systems can offset emissions by capturing biogas for energy use [237]. Incineration, though less desirable from a circular bioeconomy perspective, is technically feasible, with PHA yielding 43.5 MJ/kg of calorific energy upon combustion and producing lower toxic emissions compared to chlorine-containing plastics [238].

Beyond biodegradation, recycling represents another critical EOL pathway for PHA, enabling the retention of material value and supporting circular bioeconomy objectives. Mechanical recycling is the simplest approach, involving the collection, re-extrusion, and remoulding of PHA products [238]. However, repeated thermal-mechanical processing induces chain scission and changes in crystallinity, leading to rapid deterioration of properties. Studies show that the tensile strength of P(3HB) blends drops below 50 % after just three extrusion cycles, limiting their long-term recyclability [239]. Additives or compatibilizers can partially mitigate this, retaining up to 80 % of the properties, but recyclability remains limited to a few cycles [238]. Chemical recycling offers a more promising route for achieving closed-loop circularity. Pyrolysis at 400–500 °C, solvolysis under milder conditions, and emerging supercritical CO₂ methods enable depolymerisation back to high-quality monomers that can be repolymerized into new PHA with recovery yields of up to 85 % [240]. These strategies not only conserve material value but also reduce the need for resource- and energy-intensive de novo biosynthesis. However, despite standards such as ASTM D6400 in the U.S. and the EU Circular Economy Action Plan, enforcement of compostable plastics regulations is inconsistent, and

Table 2

Patents related to applications of PHA across various industries.

Patent no	Invention	Highlight(s)	Assignee	Reference
CA3074733C	Calendered surgical meshes comprising polyhydroxyalkanoates	Resorbable calendered surgical meshes from P(4HB) or its copolymers, with reduced thickness and smooth surface for pelvic organ prolapse repair	Tepha Inc	[196]
CN116218173B	A packaging bag material with strong antibacterial properties and a preparation method thereof	Biodegradable PHA-based packaging bag with additives for strong antimicrobial activity, fast degradation, and improved preservation	Shenzhen Dinglisheng Technology Co Ltd	[197]
CN115785637B	Foaming material and preparation method thereof	Foaming material from crystalline–amorphous PHA for biodegradable packaging, sport shoe sole, biomedical microporous foams, etc	Beijing Micro Structure Factory Biotechnology Co Ltd	[198]
CN116218180B	Flame-retardant material	Flame-retardant PHA material with phosphorus–nitrogen additive for high-safety applications in building, textiles, aerospace, automotive, and packaging	Beijing Micro Structure Factory Biotechnology Co Ltd	[199]
CN115920126B	Polyhydroxyalkanoate microsphere loaded with plant exosomes and preparation method thereof	Rough-surfaced PHA microspheres loaded with plant-derived exosomes for targeted delivery and regenerative medicine applications	Guangzhou Yuanxiang Medical Biotechnology Co Ltd	[200]
CN111801385B	Shaped objects, sheets, and containers, as well as tubes, straws, cotton swabs, and balloon stems	Biodegradable molded article from aliphatic polyester, PHA, and 15–50 % inorganic filler, designed for enhanced strength and performance in sustainable products	Mitsubishi Chemical Corp	[201]
CN116333378B	Polyhydroxyalkanoate microsphere composite gel and preparation method and application thereof	PHA microsphere composite gel for medical and cosmetic use.	Zhuhai Medfa Biotechnology Co Ltd	[202]
CN109999222B	Preparation method of nerve conduit material based on polyhydroxyalkanoate/sodium alginate electrospun nanofibers	Electrospun PHA/sodium alginate nanofiber nerve conduit with chitosan-gelatin substrate, with improved processability, biocompatibility, and potential in nerve regeneration	Dalian Polytechnic University	[203]
CN111205603B	Biodegradable mulch film and preparation method thereof	Biodegradable agricultural mulching film from modified PHA with PBT-co-succinate, compatibilizer, and chain extender. For large-scale farming applications	China Petroleum and Chemical Corp, Sinopec Shanghai Research Institute of Petrochemical Technology	[204]
CN111205604B	Ultrathin high-strength high-toughness biodegradable mulch film material, film, preparation method and application	Fully biodegradable ultra-thin mulch film from PHA block copolymer, poly (butylene terephthalate-co-adipate), and performance-enhancing additives	China Petroleum and Chemical Corp, Sinopec Shanghai Research Institute of Petrochemical Technology	[205]
CN107001615B	Polymer film and anti-blocking material obtained using the same	Ultra-thin (10–1000 nm) polymer film from a block copolymer of branched polyalkylene glycol and PHA, for tissue adhesion and flexibility to accommodate body movement and surface irregularities	Toray Industries Inc., Nanotheta Co Ltd	[206]
CN113616604B	A kind of injectable polyhydroxyalkanoate microsphere and preparation method thereof	Injectable PHA microspheres prepared via an oil-in-water process with hyaluronic acid, for soft-tissue augmentation and other biomedical filler applications	Beijing Jingyan Biomaterial Technology Co Ltd	[207]
ES3029739T3	Biodegradable coatings based on aqueous phase dispersions	Biodegradable aqueous PHA dispersion (35–75 % water, 25–65 % PHA) used to coat biodegradable food-service articles, for protective performance.	Danimer Ipco LL	[208]
EP3180040B1	Self-retaining sutures of poly-4-hydroxybutyrate and copolymers thereof	Self-retaining absorbable sutures from P4HB or copolymers with enhanced tensile strength for secure wound closure	Tepha Inc	[209]
FR3146686B1	Biodegradable polymer for 3D printing	PHA blend composite reinforced with calcareous algae for coral reef restoration, 3D-printing filaments, and coral-holding devices	Corail Artefact Science & Tech	[210]
FR3121353B1	Cosmetic composition comprising at least one polyhydroxyalkanoate	Tailored PHA copolymer cosmetic composition, as film-forming agents with long-lasting effects and strong adhesion to keratin-based materials such as skin, hair, and nails	Polymaris Biotechnology, SAS Chanel Parfums Beaute SAS	[211]
JP7259036B2	Cosmetic composition containing polyhydroxyalkanoate in an oily medium	PHA is incorporated in an oily medium for use as a film-forming agent in treating keratinous materials, enabling applications in make-up products such as mascara, eyeliner, eyeshadow, and lipstick	LOreal SA	[212]
US11896741B2	Process for preparing a polarised film or sheet containing β -form polyhydroxyalkanoate-based copolymer	A device with β -form PHA-based copolymer layer (10–99 % by XRD) in electrospun or polarised form, exhibiting piezoelectric, pyroelectric, or ferroelectric effects for use in sensors, actuators, nanomotors, or biobatteries	University of Delaware	[213]
US11433007B2	Powdered compositions based on polyhydroxyalkanoates and uses thereof in dental prophylaxes	Biodegradable PHA–silica powder (1–100 μ m), safe for air-polishing teeth and for general oral care	Bio On SpA	[214]
US11306202B2	A composition based on at least one biodegradable polymer, and use as a binder for coating products	A binder from PHA with saturated side chains dissolved in aromatic solvents for coating products	Bio On SpA	[215]
US12262640B2	Piezoelectric device comprising a membrane comprising fibres of a polyhydroxyalkanoate	A piezoelectric device with electrospun PHA fibres and piezoelectric oxides suitable for micro-actuators, drug delivery, and tissue engineering	Bio On SpA	[216]
US12285325B2	Absorbable implants for plastic surgery	Absorbable, shape-conforming P4HB or copolymer breast implants for tissue regeneration, host tissue in-growth, and minimally invasive reconstruction or mastopexy	Tepha Inc	[217]
US11241375B2	Cosmetic composition comprising biodegradable polymers	Cosmetic composition containing 1–5 % PHA and a latex polymer, suitable for eyelash applications	LOreal SA	[218]

(continued on next page)

Table 2 (continued)

Patent no	Invention	Highlight(s)	Assignee	Reference
US11866606B2	Biodegradable coatings based on aqueous PHA dispersions	Aqueous dispersion of PHA (25–65 % PHA) for eco-friendly coatings on food-contact items	Danimer Ipco LLC	[219]
US10590289B2	Use of polyhydroxyalkanoates as additives in coating compositions	Use PHA as additives (matting agents) in coating solution with controlled gloss reduction and desirable surface appearance when applied	Altana Pharma BV	[220]
US11332612B2	Polyhydroxyalkanoate particles and aqueous dispersion of the same	PHA particles coated with peptidoglycan (0.1–1.0 %) for improved aqueous dispersibility, film formation, odour suppression, and color quality	Kaneka Corp	[221]

regional recognition of composability varies [241]. Many regions still lack industrial composting infrastructure, leading to compostable products ending up in landfills or contaminating recycling streams [241]. Fragmented labelling and certification schemes lead to consumer confusion and limit effective implementation [242]. These challenges highlight the need for harmonised global policies to fully realise the circular potential of PHA and other compostable bioplastics.

8. Future prospects and concluding remarks

In recent years, significant progress has been made in expanding microbial production platforms, valorising low-cost and waste-derived feedstocks, and advancing environmentally benign recovery methods. As highlighted in this review, integrating extremophile-based non-sterile fermentations, precision metabolic engineering, synthetic microbial consortia, and CO₂- or methane-fed autotrophs presents transformative opportunities to decouple PHA production from expensive substrates and stringent process controls. Parallel advances in green solvents, supercritical fluid extraction, and biological recovery further promise reduced environmental footprints while enhancing polymer quality. Nevertheless, critical research gaps remain, which include scaling up production processes without compromising cost-efficiency or sustainability, achieving consistent monomer composition in mixed microbial cultures, and devising strategies for co-producing high-value by-products alongside PHA. Addressing these issues will require a focus on utilising inexpensive, renewable feedstocks, such as volatile fatty acids from anaerobic digestion. These feedstocks can be leveraged within mixed microbial cultures and dynamic bioreactors, with the support of synthetic biology tools like CRISPR/Cas and dynamic regulatory circuits. Likewise, multi-omics and machine-learning-guided strain selection, combined with process intensification strategies including real-time monitoring and automation, will enhance industrial scalability. Downstream, innovations such as engineered lytic enzymes, secretion-based recovery, and novel green extraction technologies can reduce energy demand and environmental impact. Additionally, tailoring polymer properties through enzyme engineering and synthetic control of monomer composition can influence high-value applications. Digitalisation and AI-driven modelling will enhance predictive control, quality assurance, and risk mitigation. By coupling biotechnological innovation with techno-economic and life-cycle assessment insights, PHA can evolve from niche materials into cornerstone components of a sustainable, low-carbon global plastics economy.

CRediT authorship contribution statement

Theresa Yetunde Fadipe: Writing – original draft, Visualization. **Ayodeji Amobonye:** Writing – review & editing, Project administration, Conceptualization. **Santhosh Pillai:** Writing – review & editing, Supervision, Resources, Funding acquisition, Conceptualization.

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Declaration of competing interest

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

Data availability

Not applicable.

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