Jurnal Pijar MIPA
https://jurnalfkip.unram.ac.id/index.php/JPM

ISSN 1907-1744 (Print)
ISSN 2460-1500 (Online)

Polyhydroxyalkanoates (PHA) Polymers from Nature for Nature: Structure, Synthesis, and Applications

Aruna Akbar Zhafransyah[1*], Annisa Mamluaturrahmatika[2], Natalia Nada Maharani[3]

[1]Department of Chemistry Education Department, Faculty of Teacher Training and Education, University of Mataram, Mataram, Indonesia
[2]Doctoral Study Program of Chemistry Education, Faculty of Mathematics and Science, Universitas Negeri Yogyakarta, Yogyakarta, Indonesia
[3]Chemistry Department, Faculty of Science and Technology, UIN Walisongo, Semarang, Indonesia
[*]e-mail: arunazhafransyah@staff.unram.ac.id

Received: May 12, 2026. Accepted: August 31, 2026. Published: October 6, 2026

Abstract: Excessive accumulation of plastic waste is an unresolved global environmental problem. A solution that can be applied and has the potential to overcome this issue is the use of natural polymer materials, such as polyhydroxyalkanoates (PHA). PHA has good physicochemical properties and characteristics similar to those of conventional plastics, making it a viable alternative plastic matrix. The application of PHA serves as a composite and can decompose plastic waste, a major problem today. The structure, synthesis, and applications of various PHA fields will be discussed in this review, which includes previous research reviews. PHA is biodegradable because it is processed by microorganisms. PHA can be synthesised from various microorganisms and carbon sources. The application of PHA also plays a role in the pharmaceutical and biofuel fields. This review makes a significant contribution to the development of polymer applications that support the global transition towards clean and environmentally friendly energy. This review employed a systematic literature review (SLR) approach following the PRISMA framework and PICOS criteria. Of 280 records identified in the Scopus database for the 2020-2024 period, nine experimental articles met the eligibility criteria and were analyzed using structured data extraction and narrative synthesis. The synthesis indicates that PHA properties are influenced by monomer chain length and composition, while production performance depends on the microorganism, carbon source, cultivation conditions, and polymer recovery method. The selected studies demonstrate potential applications in biodegradable packaging, pharmaceuticals, biofuels, and waste valorization; however, industrial implementation remains constrained by production costs, scale-up requirements, and limited life-cycle evidence. Thus, this review contributes an integrated assessment of the relationship between PHA structure, synthesis strategy, and application potential, while identifying process optimization and industrial-scale validation as key research priorities.

Keywords: Applications; Microorganisms; Plastic; Polyhydroxyalkanoates (PHA); Polymers.

Introduction

In the era of Industrial Revolution 4.0, technology is advancing at an exponential rate, significantly impacting several industries, including manufacturing, economics, healthcare, and education [1]. On the other hand, many innovations that use different materials without explicit usage guidelines can be problematic [2].

Plastic is the most widely used material for food packaging because it is flexible, easy to shape, easy to mold, can be integrated into the production process, and can be heat-sealed [3]. Since 1950, the world's plastic production has increased rapidly, reaching approximately 450 million metric tons annually recently. Plastic is inherently convenient and has high market value, but the environmental issues posed by plastic pollution have garnered international attention. It is estimated that over 340 million tons of plastic waste are generated worldwide, with approximately 46% coming from the packaging and single-use product sector, which typically has a lifespan of only a few weeks or even days in some cases [4]. The accumulation of plastic waste is the most basic and rampant environmental issue. This problem not only impacts the ecosystem but also affects health factors. Limited technical capacity for managing hazardous waste, inadequate recycling and recovery infrastructure, and low awareness of rules and regulations are the main factors behind the accumulation of plastic waste [5].

The amount of waste can be reduced by utilizing biodegradable products [6]. With advances in science and technology, especially in polymer chemistry, the use of polymer materials is increasingly widespread in everyday life. This demonstrates the discipline's flexibility and practicality. However, the community's rising standard of living has also increased dependence on polymer materials [7]. One of the polymers synthesized from natural materials or waste is PHA, further study of PHA can function as a plastic mixture so that it is easily decomposed and minimizes the accumulation of plastic waste [8]. Polyhydroxyalkanoates (PHA) are biodegradable polymers produced by various types of bacteria as storage compounds within intracellular granules. PHAs are biopolymers that can effectively replace conventional petrochemical-based plastics because they have material properties comparable to those of plastics [9].

How to Cite:
A. A. Zhafransyah, A. Mamluaturrahmatika, and N. N. Maharani, "Polyhydroxyalkanoates (PHA) Polymers from Nature for Nature: Structure, Synthesis, and Applications", *J. Pijar.MIPA*, vol. 21, no. 5, pp. 950–962, Oct. 2026. https://doi.org/10.29303/jpm.v21i5.12089

Microorganisms can produce PHAs in various ways, and their uses extend beyond plastic composites to other industries. Science process skills, such as the capacity to recognize and solve problems and ask questions about natural phenomena, are essential foundations in the context of technology development [10]. These skills foster the methodical and analytical thinking processes necessary for research-based innovation. As a result, the development of science process skills not only enhances scientific knowledge but also strategically drives the emergence of new, sustainable, and adaptive technologies. As a result, this paper examines the structure, synthesis, and applications of PHAs through a review of prior research and the literature, and offers recommendations for further research.

Previous reviews have generally emphasized individual aspects of PHA, including production development, biodegradability, microbial synthesis and degradation pathways, material properties, or end-of-life options [8], [9], [12], [14], [23]. However, an integrated comparison linking PHA monomer and polymer structures with microbial synthesis conditions and the suitability of the resulting materials for specific applications remains limited. The relative advantages and limitations of different microorganisms, carbon sources, extraction methods, and application contexts have also not been critically synthesized within a single analytical framework. Accordingly, the novelty of this review lies in systematically examining recent experimental studies from an integrated structure-synthesis-application perspective and in identifying the technological, economic, and sustainability challenges that will influence future PHA development.

Research Methods

This literature review used the systematic literature review (SLR) method to review and analyze previous studies related to the structure, synthesis, and applications of polyhydroxyalkanoates (PHA) polymers. The Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) framework was used to support transparency and accuracy during the article selection process. The review process was carried out through identification, screening, eligibility assessment, inclusion, data extraction, and narrative synthesis stages.

To minimize selection bias, the research focus and eligibility criteria were formulated using the PICOS framework. The main research question was: How are the structure, synthesis, and applications of PHA polymers described in recent experimental studies? In this review, the PICOS components comprised: (P) polyhydroxyalkanoates (PHA) polymers and PHA-producing microorganisms; (I)saba PHA synthesis, extraction, characterization, and application in modern life; (C) differences in microorganisms, carbon sources, synthesis methods, or application contexts where available; (O) PHA structure, synthesis process, physicochemical properties, and applications in packaging, pharmacy, biofuel, or waste-based production; and (S) experimental research articles.

In the identification stage, the literature search was conducted in Scopus. The keywords used were "Polyhydroxyalkanoates" "structure" "synthesis" "applications". The search was limited to articles published in 2020-2024, written in English, open access, and categorized as experimental research articles. A total of 280 records were obtained from the initial search, and 9 articles met the predetermined inclusion criteria. Figure 1 shows the review process using the PRISMA framework, while Table 1 presents the search query and search results.

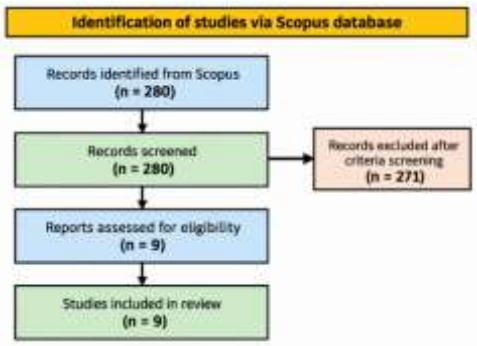


Figure 1. Review Process Using the PRISMA Framework

Table 1. Search Queries and Search Results

Search period: 2020-2024			
Database	Search query	Filter setting	Search result
Scopus	"Polyhydroxyalkanoates" AND "structure" AND "synthesis" AND "applications"	Year: 2020-2024; experimental research article; English; open access	9
Total	Total	Total	9

In the screening stage, the titles, abstracts, keywords, and full texts of the retrieved articles were examined according to the predetermined inclusion and exclusion criteria. Articles that were not directly related to PHA structure, synthesis, or applications; articles outside the publication period; non-experimental studies; non-English articles; and articles without open-access full text were excluded. The inclusion and exclusion criteria used in this review are shown in Table 2.

Table 2. Inclusion-Exclusion Criteria

Inclusion Criteria	Exclusion Criteria
Published in 2020-2024	Published outside 2020-2024
Indexed in the Scopus database	Not indexed in the Scopus database

Related to PHA structure, synthesis, and/or applications	Not related to PHA structure, synthesis, and/or applications
Experimental research article	Review, meta-analysis, bibliometric study, editorial, or other non-experimental article
Written in English	Written in languages other than English
Open-access article with full text available	Full text unavailable or not open access

The eligible articles were then extracted using a structured data extraction matrix containing the author, year of publication, microorganism, carbon source, synthesis or extraction method, research purpose, research conclusion, and application area. The extracted data were rechecked against the original articles to maintain consistency. Finally, the selected studies were synthesized narratively and organized into three main discussion themes: PHA structure, PHA synthesis, and PHA applications.

To strengthen methodological rigor, the nine eligible studies were critically appraised using an eight-domain checklist adapted from the JBI critical appraisal tool for quasi-experimental studies [51]. The domains assessed were clarity of the research objective; appropriateness of the experimental design; description of microorganisms, substrates, and cultivation conditions; inclusion of controls or comparative/optimization conditions; validity and reproducibility of analytical methods; reporting of replication and statistical analysis; completeness of the results; and consistency between the data and conclusions. Each domain was rated as yes, no, or unclear. Studies meeting seven to eight domains were classified as high quality, five to six as moderate quality, and zero to four as low quality. Studies were not excluded solely on the basis of quality; instead, appraisal results were used to weight the interpretation of production, material-property, and application claims.

The data-extraction matrix was expanded to record study design, microbial strain, substrate or carbon source, cultivation mode and conditions, recovery or extraction technique, PHA concentration or cellular content, polymer composition, characterization method, intended application, and reported limitations. Quantitative data were retained in the units reported by the original studies and were not statistically pooled because the studies used heterogeneous strains, substrates, reactor scales, cultivation times, recovery procedures, and outcome definitions. Narrative synthesis was therefore performed by comparing studies within three evidence groups: structure and molecular regulation, microbial production and recovery, and material properties and applications. Convergent findings were summarized as cross-study patterns, whereas differences in yield, polymer composition, process scale, and analytical scope were treated as sources of heterogeneity. The reduction from 280 records to nine included studies resulted from the deliberately narrow eligibility criteria, particularly the combined focus on experimental PHA research published in 2020-2024, Scopus indexing, English language, open-access full text, and direct relevance to structure, synthesis, or application. This strict selection improved full-text traceability and permitted detailed extraction, but it also reduced breadth and may have excluded relevant non-open-access or differently indexed studies. Accordingly, this review should be interpreted as a focused systematic synthesis rather than a comprehensive meta-analysis. One included study investigated the *cyanophycin granule polypeptide* rather than PHA directly [31]; it was retained only as a comparative example of high-value microbial polymer recovery from activated sludge and was not used as direct evidence of PHA production performance.

Results and Discussion

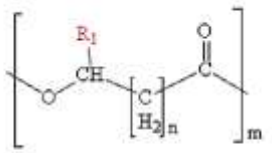
PHA Structure

Polyhydroxyalkanoates (PHA) are a group of biocompatible and biodegradable polyesters with various chemical structures, making them one of the significant bio-based materials. These compounds can be synthesized and stored by various types of microorganisms as energy reserves and carbon, especially when experiencing stressful environmental conditions. It has environmentally friendly properties, such as biodegradability and biological compatibility [11].

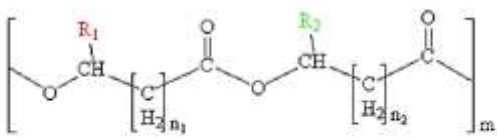
Polyhydroxyalkanoates (PHA) are a type of biodegradable plastic that has great potential and can be synthesized by various types of microorganisms by utilizing various substrates derived from waste as raw materials [12]. PHA is composed of the elements H, C, and O obtained from the metabolism of renewable resources such as lipids, carbohydrates, and other substances. The PHA monomer unit will affect the polymer's physical properties; degradable polymers exhibit distinct properties [13]. The PHA structure consists of monomer units (R)-*hydroxy fatty acids* connected by ester bonds. Each monomer unit has a side chain R group, namely a substituted alkyl group, a branched alkyl group, and a saturated alkyl group or an unsaturated alkyl group [14].

$$[\ -O-CHR-CH2-CO- \ ]_n$$

Based on the number of carbon atoms in the monomer unit, PHA is classified into three classes, namely short-chain PHA (SCL), medium-chain (MCL), and long-chain (LCL) [13], [14]. PHA, based on its structure, is classified into two, namely homopolymers and copolymers [12].



Homopolymers PHA



Copolymers PHA

Figure 2. PHA structure [12]

Natural polyesters called PHA (Polyhydroxyalkanoates) are distinguished by the length of the carbon chain in their constituent monomers. Short-chain PHAs consist of 3-5 carbon atoms, such as PHV (poly(3-hydroxyvalerate)) and PHB (poly(3-hydroxybutyrate)) produced by the bacteria Cupriavidus necator. However, this type tends to be stiff and brittle, making it less suitable for applications such as biomedical films and packaging due to its limited mechanical properties [15]. Meanwhile, medium-chain PHAs have 6-14 carbon atoms, for example, PHO (poly(3-hydroxyoctanoate)) produced by *Pseudomonas mendocina*. This type is more flexible (elastomeric), but it has low mechanical strength. Long-chain PHAs, such as poly(3-hydroxypentadecanoate) produced by *Pseudomonas aeruginosa*, have monomers with 15 or more carbon atoms [16].

Further identification revealed that PHA exists as granules, as shown in Figure 4 and Table 3. PHA granules are round or oval-shaped intracellular inclusions synthesized by various bacteria as energy and carbon reserves. These granules consist of a PHA polymer core surrounded by a protein and phospholipid layer, including the enzyme PHA synthase and structural proteins such as phase [17].

Table 3. Characteristics of PHA Granules

Characteristics	Description
Measure	0.2-0.5 micrometers (μm), can reach 1 μm depending on the type of bacteria
Shape	Round, oval, or sometimes irregular
Location	In the bacterial cytoplasm
Main composition	PHB, PHBV, or other PHA mixtures
Surrounded by	Protein layer (phasine), PHA synthase enzyme and degradation
Optical properties	Birefringent (appears bright under a polarizing microscope)

[18]

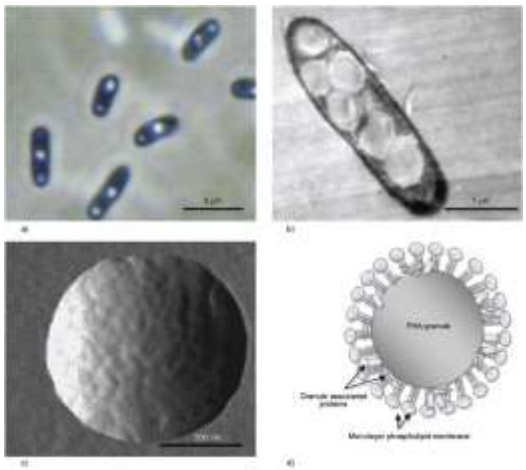


Figure 3. Morphology of PHA granules in bacterial cells observed using (a) Phase contrast microscopy, (b) Transmission Electron Microscopy (TEM), (c) Atomic Force Microscopy (AFM) deflection image showing the presence of globular particles on the granule surface, (d) Model of natural PHA granules depicting the presence of a protein monolayer on the granule surface [19]

Taken together, the structure-focused evidence indicates that polymer composition, rather than the PHA designation alone, determines material performance. Short-chain PHAs, such as PHB, generally exhibit high crystallinity and stiffness but limited flexibility, whereas medium-chain-length PHAs offer greater elasticity but lower mechanical strength. Copolymerization and in vivo blending can reduce brittleness and broaden the processing window [29], [30]. Thus, production strategies that control the proportions of 3HB, 3HV, 4HB, or medium-chain-length monomers provide a direct link between microbial metabolism, polymer structure, and application-specific mechanical and degradation behavior.

PHA Synthesis

Polyhydroxyalkanoates (PHA) can be synthesized directly by microorganisms through the fermentation of carbon substrates. Microorganisms and cultivation conditions of homo- or copolyesters with different hydroxyalkanoic acids determine the PHA synthesis process [20]. In addition to these two things, other factors that affect PHA synthesis are PHA concentration, carbon source, temperature and pH, and type of microorganism [21]. Microorganisms commonly used in PHA synthesis include *Cupriavidus necator*, *P. aeruginosa*, *Pseudomonas*, *Halophilic Bacillus sp*, and others [22]. In PHA synthesis, the intake of carbon substrates by microorganisms utilizes carbon sources such as glucose, fatty acids, or organic waste (eg cooking oil) as raw materials for PHA synthesis and the formation of PHA monomers [23]. According to [12], commonly used carbon sources are divided into five categories, namely gas, n-alcohol (such as ethanol, methanol, octanol, and glycerol), carbohydrates (sucrose, fructose, maltose, glucose, lactose, cellulose, starch, and xylose), n-alkanoic acids (propionic acid, acetic acid, valeric acid, butyric acid, hexanoic acid, oleic acid, and lauric acid), and n-alkanes (dodecane, octane, and hexane). In addition to carbon sources, nitrogen sources are also needed [22]. Nitrogen and carbon have different effects on the overall PHA production rate in different microbial strains. The positive effect on the PHA production rate is due to nitrogen concentration being limited while the carbon substrate is increased.

PHA bacterial fermentation is carried out in a fermentation vessel filled with growth media containing bacteria and mineral salts that have been sown with fermentation seeds. During fermentation, the carbon source is provided until it runs out, cell development is complete, and PHA accumulation is complete. The fermentation time lasts for 38 and 48 hours. An important step in PHA

synthesis is the separation and purification of polymers from microorganisms. Organic solvents must be used to chemically extract microorganisms. The solubility and insolubility of PHA in a particular solvent system are the basis for extraction techniques [20]. The scheme of microorganisms and extraction techniques in PHA synthesis is shown in Table 4.

Table 4. Microorganism scheme and extraction techniques in PHA synthesis

Microorganisms	Method	Research Purposes	Research Conclusions	Reference
Transgenic E. coli	FTIR Spectroscopy	Exploration of *polyhydroxyalkanoate* (PHA) biosynthesis genes in wild-type yeast strains highlighted the remarkable capabilities of isolate DMG-2.	Pioneering efforts to explore PHA biosynthesis genes in yeast cells using isolate DMG-2 showed tremendous potential.	[24]
P. aeruginosa	Solvent extraction with dichloromethane	Medium-chain polyhydroxyalkanoates (mcl-PHA) are biopolyesters derived from renewable biomass resources, such as palm oil, and can be converted into value-added products, including biopolymers that can increase the economic value of crude palm oil.	Palm oil is a good renewable and economical carbon feedstock for mcl-PHA production by *P. aeruginosa.*	[22]
P. aeruginosa strain EO1	Hypochlorite and chloroform solvent extraction	Using cheaper vegetable oils as carbon sources helps reduce the cost of biopolyester production. Various vegetable oils, including peanut oil (GNO), mustard oil, sesame oil, and soybean oil (SBO), were used in this study to assess their effects on PHA production by *Pseudomonas aeruginosa EO1* (MK049902).	Peanuts have high potential for oil production and diversified by-products that enable value aggregation. A perennial, sustainable species like this will almost certainly meet the criteria to become a significant commercial oil crop.	[26]
Pseudomonas aeruginosa	Solvent extraction	This study aims to produce PHA from Pseudomonas aeruginosa using agricultural waste as a carbon source.	*Pseudomonas aeruginosa 0L405443* is a local bacterial strain utilized for PHA production using sustainable, readily available, and affordable agricultural waste hydrolysate as a substrate.	[27]
Cupriavidus necator	Centrifugation	The main objective of this study was to assess and improve fermentation conditions for producing polyhydroxyalkanoates (PHAs), such as *poly*(3-*hydroxybutyrate*) homopolymer (PHB) and *poly*(3-*hydroxybutyrate-co*-3-*hydroxyvalerate*) copolymer (PHBV), from renewable and inexpensive industrial waste using the wild bacterium *Cupriavidus necator*.	The use of residual glycerol as an ideal raw material for PHA production by wild-type *C. necator* strains.	[28]
Aneurinibacillus sp.	Chloroform extraction	In-depth material analysis of PHA polymers produced by *Aneurinibacillus sp. H1* to elucidate how monomer composition influences fundamental structural and	*Aneurinibacillus sp. H1* is a promising candidate for thermophilic PHA production with tunable material properties and chemical composition	[29]

		physicochemical parameters of the material in solvent-cast film form.	through appropriate adjustments to the cultivation process.	
Pseudomonas umsongensis	Centrifugation	Subcellular localization of the resulting polymers was analyzed by fusing the scl- and mcl-PHA markers to fluorescent proteins.	The thermal and mechanical properties of PHB can be enhanced by blending with mcl-PHA, which acts as an efficient plasticizer. This capacity in bacterial strains represents a novel in vivo strategy for creating PHA blends with targeted properties, either through raw material design or strain engineering.	[30]
Cyanophysin Granule Peptide (CGP)	Metagenomics and metatranscriptomics	Analysis of *cyanophysin granule peptide* (CGP) synthesis in activated sludge and its adsorption capacity towards heavy metals and dyes.	The abundance and expression levels of CGP synthase (cphA) were similar to those of *polyhydroxyalkanoate polymerases*, implying high CGP synthesis in activated sludge.	[31]
R. eutropha Re2058/pCB113	Liquid chromatography and tandem mass spectrometry	Promoter pulldown assay with crude protein extract from *R. eutropha Re2058/pCB113* to identify potential transcriptional regulators involved in the control of PHA metabolic expression, specifically targeting the phasin gene phaP1 and the depolymerases phaZ3 and phaZ5.	New insights into the regulation of PHA metabolism in R. eutropha, revealing specific interactions of novel transcriptional regulators.	[25]

Critical Appraisal of the Included Studies

The appraisal showed that the included studies were generally methodologically adequate but differed markedly in direct relevance to the review question. Studies using controlled optimization, multiple analytical methods, statistical testing, or complementary in vivo and in vitro validation were given greater interpretive weight. Studies focused primarily on molecular regulation or material characterization were used to explain biosynthetic and structure-property mechanisms rather than production efficiency. The activated-sludge CGP study [31] was methodologically robust but indirect for PHA and therefore contributed only contextual evidence. No included study combined standardized productivity reporting, pilot-scale validation, techno-economic analysis, and complete life-cycle assessment.

Table 5. Methodological quality appraisal of the included studies

Study	Main evidence used in this review	Appraisal	Limitation influencing interpretation
Tanikkul et al. [22]	Flask-scale mcl-PHA production from palm oil with FTIR and GC-MS confirmation.	Moderate	One strain and small-scale batch design; no extraction-cost, scale-up, or life-cycle analysis.
Abd-El-Haleem et al. [24]	Yeast screening, gene discovery, and physicochemical confirmation of PHA.	High	Strong molecular evidence, but no standardized titer, productivity, or pilot-scale production data.
Santolin et al. [25]	Molecular regulation of PHA metabolism using pull-down, LC-MS/MS, reporter, and binding assays.	High	Mechanistic study; not designed to compare production yield or application performance.
Mahato et al. [26]	Optimization of oil-based PHA production and polymer characterization.	Moderate	Quantified cellular PHA, but laboratory scale and solvent-intensive recovery limit industrial inference.

Study	Main evidence used in this review	Appraisal	Limitation influencing interpretation
Oyewole et al. [27]	Agrowaste hydrolysate utilization and response-surface optimization.	Moderate	Quantitative results were reported in several units, with a maximum scale of 10 L.
Nygaard et al. [28]	PHB and PHBV production from residual glycerol using batch and fed-batch strategies.	High	Feedstock composition may vary, while economic performance and larger-scale recovery were not assessed.
Sedlacek et al. [29]	Detailed structure-property analysis of thermophilic PHA copolymers.	High	Production productivity was not the primary endpoint, limiting direct comparison with fermentation studies.
Cerrone et al. [30]	In vivo scl-/mcl-PHA blending and evaluation of material properties.	High	Industrial productivity, long-term processing stability, and cost were not reported on a common basis.
Zou et al. [31]	Recovery and characterization of CGP from activated sludge.	High (indirect)	The target polymer was CGP, not PHA; the study was used only as comparative evidence for bioresource recovery.

Comparative Synthesis of Microorganisms, Carbon Sources, and Production Outcomes

Production-focused studies differed in microorganism, substrate, cultivation mode, measurement unit, and downstream recovery. Table 6 therefore presents the reported values without statistical pooling and distinguishes production performance from mechanistic or material-property evidence.

Table 6. Cross-study comparison of PHA production and related evidence

Microorganism and study	Carbon source or process	Key reported outcome	Comparative advantage	Main limitation
P. aeruginosa TISTR 1287 [22]	Palm oil; 0.75% (w/v), 30 degrees C, 72 h.	0.65 g/L PHA and 38.02% cellular content.	Renewable feedstock and production of heterogeneous mcl-PHA.	Low titer and flask-scale evidence; no complete recovery-cost assessment.
P. aeruginosa EO1 [26]	Groundnut oil; 2% (v/v), pH 7, 35 degrees C, 72 h.	58.41% PHA with 10.5 g/L dry cell weight.	Highest reported cellular PHA fraction among the oil-based studies.	Edible oil and hypochlorite/chloroform recovery may constrain sustainability and scale-up.
P. aeruginosa OL405443 [27]	Sugarcane-bagasse hydrolysate; pH 6.5, 38 degrees C, 24 h, 3% carbon source.	5.86 mg/mL during substrate comparison; 10.57 g PHA from 10 L under optimized conditions.	Uses non-food agrowaste and achieved a comparatively short optimum cultivation time.	Pretreatment and enzymatic hydrolysis add complexity; outcomes are not reported in the same units as those of other studies.
C. necator [28]	Untreated residual glycerol; batch PHB and propionic-acid-fed PHBV production.	Up to 4.1 g/L PHB and 3.4 g/L PHBV, with 3HV up to 12 mol%.	Valorizes biodiesel waste and enables copolymer-composition control.	Requires strain adaptation and controlled feeding; residual-glycerol composition may vary.
Aneurinibacillus sp. H1 [29]	Thermophilic cultivation with adjustment of monomer precursors.	Tunable 3HB/4HB/3HV copolymers with controllable crystallinity and degradation behavior.	Thermophilic production and application-oriented control of material properties.	The material study did not provide a directly comparable production titer or productivity metric.
P. umsongensis GO16 [30]	Waste-derived substrates and in vivo scl-/mcl-PHA blending.	PHA blends with improved thermal and mechanical behavior; no common-basis titer extracted in this review.	Links strain engineering and granule-level blending to improved properties.	Productivity, recovery efficiency, and economic performance remain insufficiently standardized.

Microorganism and study	Carbon source or process	Key reported outcome	Comparative advantage	Main limitation
H. valbyensis DMG-2 [24]	Yeast screening, genomic-library analysis, and physicochemical characterization.	PHA presence supported by staining, microscopy, FTIR, and molecular analysis.	Introduces a distinct eukaryotic biosynthetic route and candidate genes.	No standardized production titer, yield, or pilot-scale validation.
R. eutropha Re2058/pCB113 [25]	Promoter pull-down, LC-MS/MS, reporter assays, and electrophoretic mobility-shift assays.	H16_B1672 bound the phaP1 promoter with a reported K_D of 175 nM and repressed expression.	Identifies regulatory targets for future strain engineering.	Mechanistic evidence rather than a direct comparison of PHA production performance.

A direct productivity ranking is not valid because outcomes were reported as g/L, mg/mL, percentage of dry cell weight, or molecular and material endpoints. Among the production-focused studies, *P. aeruginosa EO1* reported the highest cellular fraction at 58.41% [26], whereas *C. necator* produced up to 4.1 g/L PHB and 3.4 g/L PHBV from residual glycerol [28]. The agrowaste study reported 5.86 mg/mL for sugarcane bagasse and 10.57 g from a 10-L culture under optimized conditions [27]. These values cannot be interpreted as a single performance hierarchy because cultivation time, biomass concentration, extraction recovery, and outcome definitions differed. Nevertheless, a consistent pattern emerged: hydrophobic oils favored mcl-PHA accumulation in *Pseudomonas*, residual glycerol and controlled precursor feeding supported PHB or PHBV production in *C. necator*, and thermophilic or engineered strains broadened monomer composition and material performance.

Recovery methods also presented important trade-offs. Dichloromethane or chloroform extraction can facilitate polymer purification and characterization, but solvent toxicity, solvent-recovery requirements, energy consumption, and regulatory burden reduce industrial attractiveness [19], [22], [26], [29]. Hypochlorite-assisted digestion simplifies biomass removal but may affect polymer quality and generates additional chemical waste [19]. Centrifugation reported in some studies represents biomass harvesting rather than complete polymer recovery [28], [30], so an additional downstream extraction and purification stage remains necessary. Consequently, claims of low-cost PHA production based solely on inexpensive carbon sources should be interpreted with caution unless recovery yield, solvent recycling, energy use, and final polymer purity are also reported.

Other studies have shown that productive microorganisms for PHA synthesis include *P. aeruginosa*, *Halophilic Bacillus sp*., *Cupriavidus necator*, and *Aneurinibacillus sp*., as they are considered economical in PHA production [32], [27]. The microorganism *Pseudomonas aeruginosa* has the potential to enhance PHA production, support industrial-scale PHA production, and contribute to the manufacture of environmentally friendly bioplastics. This microorganism is considered economical because it is readily obtainable and can adapt to and survive in both aerobic and anaerobic environments [27].

The transformation of organic pollutants into bioresources through the activated sludge process has the potential to reduce carbon dioxide emissions from wastewater treatment plants. Efforts to identify new, high-value biopolymers from activated sludge are a strategic step in the recovery of bioresources. One such biopolymer is *cyanophycin granule polypeptide* (CGP), originally discovered in cyanobacteria and possessing unique chemical and material characteristics, making it suitable for various industrial applications such as food, pharmaceuticals, cosmetics, water treatment, and agriculture. Interestingly, activated sludge is known to have an excellent capacity to produce CGP. This compound also exhibits a higher adsorption capacity for anionic pollutants such as Cr(VI) and methyl orange than for cationic pollutants, due to its abundant guanidine groups [31].

On the other hand, research by Nygaard et al. (2023) showed that the bacterium *Cupriavidus necator* can utilize biodiesel waste as a carbon source, thus offering great potential for industrial production of environmentally friendly bioplastics using renewable and low-cost raw materials. Furthermore, *Cupriavidus necator* also functions as a microorganism in acid- or base-treated sewage sludge, which is used as an alternative carbon source [33].

Phosphate metabolism is crucial to this unique biosynthetic mechanism. The specific metabolic conditions of *H. valbyensis*, which can adapt to environments with high sugar and acid content, are thought to contribute to the formation of PHAs with distinct characteristics. These findings provide opportunities to develop more innovative metabolic engineering strategies and broaden the understanding of PHA biosynthesis across various organisms. By exploiting the unique metabolic pathway of *H. valbyensis DMG-2*, researchers can develop new approaches to producing sustainable bioplastics that are more environmentally friendly and whose properties can be tailored to specific needs. In addition, *R. eutropha* can also help increase PHA production for industrial applications [25].

Food waste, plant roots, and sewage sludge also serve as good substrates for microorganisms. Vegetable oil is an excellent substrate for PHA production and bacterial growth. However, the PHA productivity from this substrate needs to be improved to advance the process to application and commercial scale by optimizing the physical and chemical conditions, because this substrate is cheaper and easier to scale up [26]. PHA production can also be increased by using inulin from plant roots. Inulin can be used as a promising alternative carbon source for the production of PHA (polyhydroxyalkanoates) by certain microorganisms. Inulin is a natural polysaccharide mainly found in plants such as chicory, dahlia, artichoke, and agave. Chemically, inulin

consists of a chain of fructose units with one glucose unit at the end [32].

PHA Application

PHA has been widely studied and is considered a potential biomaterial for various applications, including packaging plastics, medical materials, drug delivery systems, biofuels, and food additives [11].

Eco-Friendly Food Packaging

Plastic packaging that burns can affect the environment and human health due to the chemicals it releases [34]. PHA is used as an alternative material for biodegradable food packaging. PHA-based films have good barrier properties against oxygen and water vapor and can be coated with antimicrobial agents to extend the shelf life of bakery and seafood products. The production of PHA from food waste, such as volatile fatty acids and used oils, also reduces production costs and environmental impacts [35]. In addition, the application of PHA using nanotechnology can protect food from harmful organisms [1].

The three biological advantages of polyhydroxyalkanoates (PHAs), such as biobased, biodegradable, and biocompatible, make PHAs among the most promising bioplastics for applications. Furthermore, it has been demonstrated that PHAs are fully biodegradable by microorganisms at high levels under all relevant aerobic and anaerobic conditions, including soil, saltwater, landfills, industrial compost, and household compost. *Poly*(3-*hydroxybutyrate-co*-3-*hydroxyvalerate*) (PHBV) is one of the SCL-PHAs that serve as alternatives to *polypropylene* (PP) and polyethene terephthalate (PET) in sustainable applications. The reason is that PHBV is comparable to PP in stiffness and strength, exhibits excellent crystallinity, and has good barrier properties similar to PET [36].



Figure 5. Biodegradation of PHA bottles, type BiopolTM, by incubation in sludge for 80 days [19]

Pharmacy

PHA (Polyhydroxyalkanoates) is an extraordinary group of bioplastics known for its biodegradability, biocompatibility, drug encapsulation capabilities, and ease of modification. In addition, PHA also has superior pharmacokinetics and pharmacodynamics compared to free drug therapy or other polymer-based drug delivery systems [37]. PHA-based drug nanocarriers also have the advantage of being naturally degradable into components that are non-toxic to the human body. The formulation of these nanocarriers can be done through various techniques, such as the very popular solvent emulsion-evaporation method (such as water-in-oil-in-water double emulsions and oil-in-water single emulsions), dialysis, nanoprecipitation, and in situ polymerization [38].

Biofuel Production

The increasing use of petroleum as fuel has depleted fuel reserves, so alternative fuels, such as biodiesel, are needed because they are derived from plant and animal sources and are environmentally friendly [39]. Biodiesel has advantages such as being environmentally friendly, non-toxic, renewable fuel, essentially free of carcinogenic sulfur and benzene, the result of combustion is which can be consumed by plants for the photosynthesis process (carbon cycle), can be relatively perfectly oxygenated or completely burned, non-toxic, and naturally decomposes (biodegradable) [40] - [42]. In 2016, the government set the use of B20 (a mixture of 20% biodiesel and 80% diesel) in the biodiesel industry, and this is predicted to increase to B30 in 2030 [43]. PHA can be converted into methyl hydroxyalkanoate esters via esterification, yielding liquid fuels similar to biodiesel. This provides an alternative renewable energy from biological sources that can reduce greenhouse gas emissions [44]. The use of catalysts must take into account the amount of catalyst used [45].

Production from Organic Waste

Environmental problems are among the most pressing issues that must be resolved immediately [46], [47]. The amount of waste is increasing every day, so there is a need for an intensive waste management strategy that is adequately and effectively supported [48]. As much as 41.27% of waste in Indonesia consists of organic waste, based on data from the Ministry of Environment and Forestry in 2022 [49]. The use of organic waste, such as food waste and agricultural waste, as substrates for PHA production has been investigated to improve sustainability and reduce production costs. Halophilic microorganisms have the potential to ferment these substrates to efficiently produce PHA [32]. In addition, awareness and knowledge of nanocomposite applications in agriculture need to be expanded to develop materials with greater efficacy and that are safe for the environment and living things [50].

Industrial Challenges, Sustainability, and Research Priorities

The reviewed evidence supports technical feasibility but remains predominantly at the laboratory scale. Production cost is influenced not only by the price of the carbon source but also by cultivation control, oxygen transfer, fermentation time, cell harvesting, polymer recovery, purification, solvent recycling, and wastewater treatment. Waste oils, residual glycerol, and agrowaste hydrolysates can reduce dependence on refined substrates, but pretreatment requirements, variable composition, inhibitors, seasonal availability, and downstream purification may offset part of the apparent saving. The frequent use of P. aeruginosa in the production studies also

requires careful biosafety and regulatory evaluation before the polymer is considered for food-contact or biomedical applications.

Technological readiness differs among applications. Packaging has the clearest near-term pathway because films and blends can be assessed using established mechanical, thermal, barrier, processing, and biodegradation tests, although brittleness of some short-chain-length PHAs, a narrow processing window, and price competitiveness remain important barriers [15], [36]. Pharmaceutical applications require more stringent evidence on polymer purity, residual solvents, reproducibility, toxicity, sterilization, stability, and in vivo performance [37], [38]. Conversion of PHA into fuel is technically feasible, but it competes with the polymer's higher material value and requires additional energy, catalysts, and separation processes [44], [45]. Therefore, broad claims that PHA can fully replace conventional plastics or make a major contribution to clean energy are not yet supported by the nine included experimental studies.

Life-cycle benefits should not be inferred solely from biodegradability. Environmental performance also depends on the origin of the carbon source, electricity and water demand, fermentation efficiency, recovery solvent, polymer lifetime, end-of-life conditions, and alternative uses of the selected waste stream. None of the nine studies conducted a complete cradle-to-grave life-cycle assessment or a full techno-economic analysis. Future studies should report standardized metrics, including PHA titer (g/L), intracellular content (% dry cell weight), volumetric productivity (g/L/h), substrate-to-product yield (g/g), recovery yield, polymer purity, molecular weight, energy consumption, and solvent use. Pilot-scale studies integrating non-food feedstocks, safer recovery methods, solvent recycling, and application-specific performance testing are needed before industrial competitiveness can be established.

Across the selected studies, the most consistent research direction is not the identification of a single universally superior microorganism, but the integration of strain selection, low-cost carbon sources, controlled monomer composition, and efficient downstream recovery. Molecular studies [24], [25] provide targets for metabolic and regulatory engineering; production studies [22], [26]-[28] identify promising substrates and operating conditions; and material studies [29], [30] demonstrate that monomer composition and blending determine crystallinity, flexibility, thermal behavior, and degradability. This structure-synthesis-application relationship is the principal scientific contribution of the review: application performance cannot be optimized independently of microbial metabolism, substrate selection, polymer composition, and recovery history.

Conclusion

The accumulation of plastic waste, a major problem to date, needs to be managed with practical, efficient techniques and practices. The development of polymer chemistry in the modern era can help with this problem, namely by synthesizing PHA polymers that can decompose naturally. PHA can be an alternative polymer or a composite in plastics to reduce plastic waste accumulation. Previous research studies explain that PHA is a chain polymer that can be synthesized from microorganisms from other carbon sources. PHA can also be applied in various fields, such as food packaging, pharmaceuticals, and biofuel production. Taken together, the nine experimental studies included in this systematic review show that PHA properties and potential uses are governed by the relationship between polymer structure, microbial synthesis, and processing conditions. Short-, medium-, and mixed-chain-length PHAs exhibit different rigidity, flexibility, thermal behavior, and biodegradability; these characteristics are influenced by the producing microorganism, carbon source, cultivation conditions, monomer composition, and extraction or recovery method. The main scientific contribution of this review is therefore an integrated structure-synthesis-application perspective, demonstrating that the selection of a microbial strain and production route must be tailored to the required material properties and intended application rather than assuming a single universally superior PHA production system. Although the reviewed studies demonstrate potential applications of PHA in food packaging, pharmaceuticals, biofuels, and organic-waste valorization, most of the available evidence remains at the laboratory scale. Therefore, conclusions regarding industrial and environmental superiority should remain cautious until production costs, scalability, recovery efficiency, solvent and energy demand, life-cycle impacts, market competitiveness, and application safety are evaluated systematically. Future research should prioritize pilot-scale production using low-cost waste-derived carbon sources, safer and more efficient downstream processing, standardized reporting of productivity and material performance, and techno-economic and life-cycle assessments. For chemistry and sustainability education, PHA provides a contextual example for connecting polymer structure, microbial metabolism, material properties, green chemistry, circular-economy principles, and the critical evaluation of environmentally responsible technologies.

Author's Contribution

This research is the result of collaborative contributions from all authors. A. A. Zhafransyah: contributed to the research concept and design, literature review, analysis of PHA structure and synthesis, and drafting of the manuscript. A. Mamluaturrahmatika: contributed to the systematic literature review process, article screening, data validation, analysis of PHA applications, and manuscript review and editing. N. N. Maharani: contributed to literature data extraction, organization of references, preparation of tables and figures, and refinement of the discussion. All authors participated in the discussion of the review findings, provided substantive input, and approved the final version of the article for publication.

Acknowledgements

The authors would like to thank the Chemistry Education Department, Faculty of Teacher Training and Education, Universitas Mataram; the Doctoral Study Program of Chemistry Education, Faculty of Mathematics and Science, Universitas Negeri Yogyakarta; and the Chemistry Department, Faculty of Science and Technology, UIN Walisongo for their academic support and encouragement during the preparation of this article. The authors also express their appreciation to all researchers whose published

works contributed to the development of this literature review.

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