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Leads and hurdles to sustainable microbial bioplastic production

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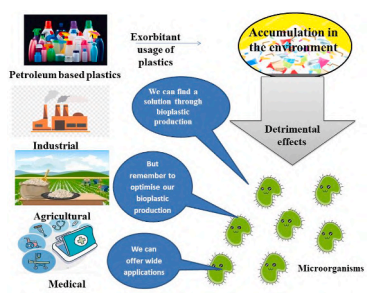
HIGHLIGHTS

- Overview of microbial bioplastics.
- Leads and hurdles of microbial bioplastics were discussed.
- Diverse applications were discussed.

GRAPHICAL ABSTRACT



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ABSTRACT

Indiscriminate usage, disposal and recalcitrance of petroleum-based plastics have led to its accumulation leaving a negative impact on the environment. Bioplastics, particularly microbial bioplastics serve as an ecologically sustainable solution to nullify the negative impacts of plastics. Microbial production of biopolymers like Polyhydroxyalkanoates, Polyhydroxybutyrates and Polylactic acid using renewable feedstocks as well as industrial wastes have gained momentum in the recent years. The current study outlays types of bioplastics, their microbial sources and applications in various fields. Scientific evidence on bioplastics has suggested a unique range of applications such as industrial, agricultural and medical applications. Though diverse microorganisms such as *Alcaligenes latus, Burkholderia sacchari, Micrococcus* species, *Lactobacillus pentosus, Bacillus* sp., *Pseudomonas* sp., *Klebsiella* sp., *Rhizobium* sp., *Enterobacter* sp., *Escherichia* sp., *Azototobacter* sp., *Protomonas* sp., *Cupriavidus* sp., *Halomonas* sp., *Saccharomyces* sp., *Kluyveromyces* sp., and *Ralstonia* sp. are known to produce bioplastics, the industrial production of bioplastics is still challenging. Thus this paper also provides deep insights on the advancements made to maximise production of bioplastics using different approaches such as metabolic engineering, rDNA technologies and multitude of cultivation strategies. Finally, the constraints to microbial

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bioplastic production and the future directions of research are briefed. Hence the present review emphasizes on the importance of using bioplastics as a sustainable alternative to petroleum based plastic products to diminish environmental pollution.

1. Introduction

Petroleum-based plastics have conquered human life daily due to their versatile, inexpensive, lightweight and excellent thermal properties. These properties have made plastics more advantageous than metals, wood, paper, etc. According to the current statistics, about 34 million tons of plastics have been produced in a year by humans, of which 7% are recycled, and the remaining 93% are dumped into the sea, oceans, and landfills, leading to its accumulation. As per reports, in 2015, more than 300 million tons of plastic were used worldwide (Sushmitha et al., 2016). Excessive usage of plastics causes severe impacts on the environment. The incineration of plastic liberates various toxic greenhouse gases, thereby contributing to global warming, climate change, and harmful effects on various species (Ford et al., 2022). Moreover, due to their high carbon footprint, petrochemical-based plastics are non-eco-friendly (Gadhave et al., 2018) and accumulate in various habitats. Plastics also incite various health issues in humans, especially the aftermaths of fluctuations in thyroid hormone levels (Darbre, 2020; Duan et al., 2021). Moreover, the synthesis of plastics also requires hazardous and carcinogenic chemical additives such as phthalate plasticizers and brominated flame retardants (Gopalakrishnan et al., 2020; Awasthi et al., 2021a).

Other forms of plastics, such as microplastics and nanoplastics also cause harmful effects on living organisms. Plastics are polymers which are made up of hydrocarbon monomers and a long-time exposure of these polymers in the environment, whether in soil or water, causes many physical and chemical changes to plastics. Mostly they may undergo depolymerization to form smaller fragments of macroplastics such as microplastics (<5 mm) and nanoplastics (<0.1 μm) (Yee et al., 2021). Apart from this, micro and nanoplastics are also synthesized for industrial applications such as exfoliants, also used in cosmetics and drug delivery particles, etc (Karbalaei et al., 2018). Nano and microplastics will find their way to the food chain when they are released to the environment and thereby cause threat to animals as well as humans. These particles may interact with proteins, lipids, carbohydrates, ions, etc of the human body (Yee et al., 2021) and thus measures to reduce plastic consumption have occurred worldwide, further promoting the recycling of plastics (Justine et al., 2015). Microplastics critically affect health, reproduction and organ development in humans as well as marine organisms; hamper the microbial flora of soil and subsequent plant growth; thereby spreading its negative impacts to different levels of the ecosystem and inhabitant life forms (Bhatt et al., 2021).

Microbes serve as double-headed swords in dealing with plastic pollution due to its ability to degrade plastic in natural environments as well as by forming a biosynthetic machinery of bioplastics as an ideal alternative to currently used petroleum derived plastics. The first plastic degradatory role of microbes is attributed to the presence of enzymes such as laccase, PeTase, esterase, lignin peroxidase, proteases, etc (Zhou et al., 2022). The diversity of these plastic remediating enzymes originated from diverse microbes in the form of bacteria and fungi, serve as effective tools to remediate petroleum-based plastics to nontoxic compounds (Dhanraj et al., 2022). The second direction of microbial role in tackling existing plastic pollution is by providing us with an eco-friendly and biodegradable range of bioplastics, to thereby reduce the use of hydrocarbon derived plastics. Since the authors have previously discussed the microbial degradation of plastics through previous publications (Dhanraj et al., 2022; Francis et al., 2021; Zhou et al., 2022), the current article concentrates on the advancements and constraints faced in microbial production of bioplastics.

Implementing novel techniques for manufacturing bioplastics that promote sustainability and reduce plastic waste has been dramatically recommended (Yadav et al., 2019). Bioplastics, unlike petroleum-based plastics, can be acquired using renewable sources and are considered novel materials of the 21st century of potential value (Chozhavendhan et al., 2020; Awasthi et al., 2021b). Since raw materials can absorb carbon dioxide throughout the growth process, bioplastic production would aid in reducing carbon emissions, further alleviating the economy's reliance on fossil fuels (Crippa et al., 2019; Kumar et al., 2021). As part of the technological progress of the bio-economy, renewable resource derived biodegradable plastics in a variety of forms such as ground film, handbags and disposable packaging are promoted (Schoenmakere et al., 2018; Duan et al., 2020; Reshmy et al., 2021).

Bioplastics, also nicknamed Green-plastics, vary in composition, existing as either starch or cellulose Polylactic acid (PLA) derivatives, and adopt diverse biodegradative pathways and biodegradation rates (Bassi et al., 2021). Bioplastics or Green plastics are named either for their formation from renewable resources or their ultimate degradability to carbon dioxide and water. Depending on the type of plastic, they can be decomposed by microorganisms to achieve alternative life cycle management, such as household composting, industrial composting, and anaerobic digestion, further encouraging the development of a circular economy (Narancic et al., 2018; Awasthi et al., 2020a). The aerobic digestion of plastics to carbon dioxide is preferred to its anaerobic digestion to methane (an approximately 20 times more potent greenhouse gas) (Quecholac-Piña et al., 2020). Moreover, it is noted that not all bioplastics satisfy both of the properties mentioned above, as some may be biobased yet not degradable to their lowest form, as in the case of bioderived polyethylene (Bio-PE) and its derivatives. Thus, the concept of American Society for testing and Materials (ASTM) D6400-21, including the 90% aerobically digestible (in 180 days) completely recyclable bioderived bioplastic specifications, has been introduced in developed countries like the United States to subcategorize bioplastics to biodegradable plastics (https://www.astm.org/d6400-21.html).

Recently, plastic manufacturers have shown a keen interest in producing bioplastics from renewable resources. This is because they can use the same processing unit, further reducing the overall investment in production infrastructure. Another striking fact is that the material properties of bioplastics are similar to the traditional polyethylene terephthalate (PET) and polyethylene (PE) resins (Amulya et al., 2015; Awasthi et al., 2020b). Brazil has successfully produced bio-based PE from sugarcane and PET using plant materials for soft drink bottle production (bioPET) (Bartolo et al., 2021). Concurrently, since 2017, industrial manufacturing of bio-remediable polybutylene succinate (PBS) using corn and sugarcane (BioPBS) has been explored (Shamsuddin et al., 2017), thus highlighting the sustainability and trends in biodegradable plastic alternatives.

Even though bioplastics are currently a tiny sector, accounting for about 1% of the global plastic manufacturing market, their production is rising. The global market for biodegradable plastics is anticipated to grow to $6.73 billion by 2025, from $3.02 billion in 2018. A primary hike in such rapid expansion directly reflects the acceptability and increased use of biodegradable alternatives in developing nations like Brazil, India, and China (Narancic et al., 2020). Although starch blends account for most biodegradable plastic manufacturing, bioplastics such as Polyhydroxyalkanoates (PHA) and Polylactic acid (PLA) residues form the leading variety of bioplastics. Their market shares are 1.2% and 13.9% (weight percentage) respectively, producing 2.11 million tons bioplastics. Global PHA production is anticipated to rise from 25,320 tonnes in 2019 to 1.59,700 tonnes in 2024, a 6.3-fold increase, while PLA production is expected to grow from 2.93,290 tonnes in 2019 to 3,

17,000 tonnes in 2024 (Narancic et al., 2020).

According to the current statistical data from the European Bioplastics Company, global bioplastic production was around 2 million tonnes in 2018, and global plastic production was about 360 million tons. In the next five years, the worldwide market for bioplastics is anticipated to increase by 40% (Bassi et al., 2021). There are already various examples of bioplastics in the market manufactured by multiple companies in Asia, Europe, and the United States. BASF (Germany), Corbion NV (Netherlands), Nature Works LLC (United States), Novamont (Italy), CJ Cheil Jedang (South Korea), and Tianjin Guoyun (China) are some of the leading producers. Nylon-11 made from castor oil and Cellophane TM made from reformed cellulose by Futamura Chemical Company (UK) were the two historically successful examples. Polylactic acid resins in different brands such as Luminy® series from Total Corbion and Ingeo TM manufactured by Nature Works LLC are the other bioplastic products available. PLA, Polycaprolactone (PCL), and copolymers are among the bioabsorbable polymers sold by Corbion under the grade PURASORB®. Danimer Scientific manufactures bioplastics based on PHA named NodaxTM, while BASF produces a variety of compostable polymers such as ecovio® and ecoflex® (Bartolo et al., 2021; Qin et al., 2021a).

The real-time scenario after Covid-19 is that it has started attacking the world as the usage of single-use plastics has been increased. It is our obligation to use protective equipment such as masks, gloves, PPE kit etc, for controlling the spread of virus and consequently, the accumulation of these single-use plastics has also increased. According to predictions, there is a chance of a two fold increase in plastic debris (Nano and microplastics) by 2030. So, by considering the implications of petroleum-based plastics, there is an urgent need to shift towards more sustainable solutions such as increased production of bioplastics (Silva et al., 2021).

This review covers all aspects from the basic to advanced methods of bioplastic production, types of bioplastics, different sources of bioplastics, types of microorganisms producing bioplastics, molecular and biochemical aspects of bioplastic synthesis, application of genetic engineering and metabolic engineering for enhanced bioplastic production and various applications of bioplastics. Hence, the present review aims to provide a detailed account of the advancements in microbial bioplastic synthesis. Signs of progress in the technologies used during the commercialization of microbial bioplastics concerning their metabolic pathways and novel applications are being discussed in the following sections. Also, this review shows how significantly bioplastic production can contribute to circular bioeconomy.

2. Types of bioplastics

Bioplastics are either bio-based or biodegradable (Yadav et al., 2019)."Bio-based" refers to a polymer entirely or partially biomass-derived polymer, such as organic waste or a renewable biological source. "Biodegradable" denotes a substance that can be metabolized microbially to carbon dioxide, water, and biomass. Based on this criterion, bioplastics are divided into three types: bio-based and biodegradable polymers (BBBP), solely bio-based polymers (SBBP) and biodegradable polymers (BP) only. PHAs, PLA, bio-PBS and polymers based on chitosan, starch, lignin, and cellulose are bioplastics with both biologically derived and biodegradable (Nampoothiri et al., 2010). Examples of bio-based bioplastics include bio-based polyethylene (bio-PE), polypropylene (bio-PP), polyamides (bio-PA), and polyethylene terephthalate (bio-PET) (Siracusa and Blanco, 2020). Lastly, PBS, polyvinyl alcohol (PVA) and polypropylene (PP) derived from fossil resources are categorized as BP varieties (Ferreira et al., 2019).

2.1. Polyhydroxyalkanoates (PHAs)

They represent a group of biopolyesters which is considered biodegradable and an optically active polymer, such as polyhydroxybutyrate (PHB), polyhroxyvalerate (PHV) and derived polymers viz, Poly(3-hydroxybutyrate-co-3-hydroxyvalerate) (PHBV) which accounts for a meagre of total bioplastic manufacture (Narancic et al., 2020; Qin et al., 2021b). Bacteria synthesize PHAs as a stress response when they lack inorganic nutrients such as oxygen, nitrogen or phosphates, while carbon is in excess amounts (Ray and Kalia, 2017). Bacterial lysis and subsequent downstream processing obtain such microbially derived intracellular fermentation products. According to Khatami et al. (2021), PHAs find various medical applications with their biocompatibility, biologically safe nature, biodegradability and ability to exhibit thermoplastic characteristics similar to petrochemical plastics. Due to their variant physical characteristics comprising diverse monomer compositions, they provide a wide range of applications. PHA has a diameter ranging from 0.2 to 0.5 μm either as5 carbon short chains or as medium chains to 14 carbons (Li et al., 2007a, b; Raza et al., 2018; Qin et al., 2021c). The physical properties of PHA depend primarily on the polymer's monomer composition, organism, growth conditions and polymer extraction techniques. Ideally, short-chained PHA has characteristics similar to traditional polymers like polypropylene and more extended PHA exhibit more elastic properties (Gopi et al., 2018).

Regardless of their differences in gram staining properties, Bacteria are equally capable of producing bioplastics. PHA production in bacteria can occur in two situations, during nutrient deficiency (deprivation of essential nutrients like nitrogen and phosphorus) and their growth phase (Khatami et al., 2021). Thus, it becomes critical to evaluate the log and lag phase of each potent PHA producer before optimization studies are

Table 1
An overview on various microorganisms producing different types of bioplastics.

Sl No.	Microorganisms used	Bioplastics Produced	Reference
1.	*Pseudomonas* spp.	PHA	Davis et al. (2013)
2.	*Burkholderia sacchari*	PHB	Cesario et al. (2014)
3.	*Burkholderia cepacia*	PHB	Pan et al. (2012)
4.	*Bacillus firmus*	PHB	Sindhu et al. (2013)
5.	*Comomonas* spp.	PHB	Sindhu et al. (2014)
6.	*Lactobacillus pentosus*	PLA	Wischral et al. (2019)
7.	Recombinant *Lactobacillus plantarum*	PLA	Zhang et al. (2016)
8.	*Pleurotus ostreatus*	Bio-ethylene	Moreno-Bayona et al. (2019)
9.	*Alcaligenes latus*	PHA	Shettar et al. (2016)
10.	*Bacillus megaterium*	PHA	Kumar et al. (2015)
11.	*Bacillus cereus*	PHA	Singh et al. (2009)
12.	*Bacillus megaterium R11 Serratia ureilytic*	PHA	Tsang et al. (2015)
13.	*Pseudomonas aeruginosa*	PHA	Israni, 2016
14.	*Comamonas testosterone*	PHA	Chen and Tan, 2014
15.	*Pseudomonas guezennei*	PHA	
16.	*Enterococcus* sp.	PHA	Chozhavendhan et al. (2020)
17.	*Brevundimonas* sp.	PHA	
18.	*Bacillus subtilis*	PHA	Chozhavendhan et al. (2020)
19.	*Micrococcus* sp.	PHB	
20.	*Rhizobium leguminosarum*	PHB	Patel and Parsania, 2018
21.	*Azotobacter beijerinckii*	PHB	Albuquerque et al. (2011)
22.	*Cupriavidus necator*	PHA	Soto et al. (2019)
23.	*Protomonas extorquens,*	PHA	Portugal-Nunes et al. (2017)
24.	*P. oleovorans*	PHA	
25.	*Saccharomyces cerevisiae*	PHB	Moreno-Bayona et al. (2019)
26.	*S. diastaticus*	PHB	
27.	*Candida krusei*	PHB	
28.	*C. tropicalis*	PHB	Simó-Cabrera et al. (2021)
29.	*Kloeckera apiculata*	PHB	
30.	*Kluyveromyces africans*	PHB	

carried. Table 1 enlists some examples of PHA producing microbes. The predominantly used PHA polymer viz. poly-3-hydroxybutyrate (PHB), is noted for its relative brittleness and high crystallinity to polypropylene. However, blending PHA monomers to produce copolymers has become common to adapt the polymer's thermal and mechanical characteristics to the required qualities by altering their composition (Ray and Kalia, 2017). PHBV with less fragility, lower melting temperature, and crystallinity percentage add to its suitability as a mould (Visakh, 2014).

Production of bioplastics is one of the circular bioeconomy approaches which can be simply defined as economic development using biological resources. In the present scenario where the after effect of development is environmental pollution, a circular bioeconomy approach with enhanced production of bioplastics is very important. Efficient utilization of bio wastes for bioplastic production is one of prime most technology in circular bioeconomy which needs to be developing more (Talan et al., 2022).

Different kinds of wastes were reported to act as excellent substrates for PHA synthesis. The main feedstocks are lignin-based wastes (Kumar et al., 2017), wastewater sludge (Kumar et al., 2018), waste water from paper, pulp and cardboard industries (Grazia et al., 2017), glycerol (Morya et al., 2018) and carbon dioxide (Kumar et al., 2016). Waste water treatment sludge can be considered as one of the potential feedstocks as they contain consortia of various microorganisms. These microbes will produce PHA in the presence of excess carbon source (Kumar et al., 2018). Glycerol as a feedstock gives a maximum yield of 85.19% of cell dry weight (CDW) PHA by using *Bacillus* sp. under optimized conditions (Morya et al., 2018). Lignocellulosic wastes generated from plants, paper and pulp industries, etc can be used by bacteria such as *Pseudomonas* sp. effectively and synthesis PHA (Kumar et al., 2020). Under optimized conditions oleaginous bacteria *Serratia* sp. showed a two-fold increased PHA production using CO_2 (Kumar et al., 2016).

2.2. Polylactic acid (PLA)

These bioplastics are biodegradable and biobased polyester synthesized via lactic acid condensation polymerization, lactide chain development, or ring-opening. In 2019, it accounted for 13.9 percent of worldwide bioplastic output (Simangunsong et al., 2019). Microbial fermentation produces PLA monomers of L or D isomers, then polymerized chemically to obtain PLA. The content of enantiomer content contributes to the physical properties of PLA regardless of its occurrence as homopolymers or heteropolymers. Homopolymers of PLA containing polyesters of either optically pure L or D lactic acid monomers will be semicrystalline, whereas PLA heteropolymers such as DL-lactic acid are amorphous (El-Hadi, 2018; Qu et al., 2021).

Corn is the best source of high-purity lactic acid. When used as starting material, plants and other woody biomass can achieve lower manufacturing costs. Increasing the concentration of raw materials can reduce production costs, but this indirectly leads to increased fermentation and saccharification costs. Ultrafiltration can be used to separate the lactate produced during fermentation. Lastly, electrodialysis can transform lactate into lactic acid. Since direct lactate condensation can only produce PLA with poor mechanical characteristics, polymerization of the intermediate dilactide is the most common method used (Brodin et al., 2017; Jain et al., 2022). In the case of microbes, large scale production of PLA is preferred by homofermentative methods because it provides a higher yield of lactic acid with fewer by-products. This method uses *Lactobacillus* sp. such as *Lactobacillus amylophilus, L. delbrueckii*, *L. leichmannii,* and *L. bulgaricus* (Chozhavendhan et al., 2020).

PLA is a biodegradable thermoplastic that may be moulded into various bio-based goods. It has been proven that PLA can be used for packaging applications reinforced with nanocellulose fibrils. Microcellulose and nanocellulose are suitable strengthening materials for PLA biocomposites (Jayakumar et al., 2021). PLA is beneficial in various aspects, such as compatibility with various fibres, excellent mechanical strength, low processing temperatures and biocompatibility compared to traditional thermoplastics. PLA is applicable in several industries, such as packaging, geotextiles, 3D printing, non-woven binder fibre, prosthetic devices, biomedical absorbable sutures, bio sorbents etc. Various sectors have commercialized PLA manufacture and other related biocomposites (Achaby et al., 2016; Malladi et al., 2018).

2.3. Polyurethane (PU)

Polyurethane is a polymer containing urethane groups in its chemical structure and are generally produced by reacting polyols containing two or more hydroxyl groups with isocyanates possessing two or more isocyanate groups. Because of their toxicity, all forms of isocyanate cannot be employed in industry for PU production. Also, while various polyols are available, the resources needed to synthesize them are largely petroleum-based, posing environmental concerns (Pfister et al., 2011). As a result, eco-friendly PU synthesis from renewable resources has attracted much interest from researchers. Innovative methods like microbial conversion of renewable feedstock to the precursor compound for producing PU have been developed. *Pseudomonas aeruginosa* was used to convert olive oil to dihydroxy fatty acids, and then those dihydroxy fatty acids were reacted with hexamethylene diisocyanate (HMDI) to form PU (Tran et al., 2018). Lignin can be an inexpensive source for manufacturing polyurethane (PU). Based on the lignin content and its nature, the mechanical properties of PU can be analyzed. Organosolv lignin (15–25 W %) produces tough PUs in its natural state, but greater lignin concentration causes the PUs to become brittle and hard. To optimize the mechanical characteristics of PU, flexible aliphatic polyols must be combined with rigid lignin polyols (Kurańska et al., 2013). Liquifying lignin polyols is another alternative to formulate a more flexible PU. Flexible polyols such as polyethylene glycol and glycerol are mixed with low molecular weight lignin fragments through enzymatic hydrolysis and other mechanical treatments, during which some self-polymerization step occurs. PU is utilized in various products, including electronic and automotive goods bedding, construction, furniture binders and foams and coatings. Lignin may also be used to make phenol-formaldehyde resins, which can quickly form thermoset polymers. Hence, lignin can be utilized as a bio-based alternative to produce bioplastics (Kurańska et al., 2013; Hoeng et al., 2016; Sarsaiya et al., 2019).

3. Organisms producing bioplastics

3.1. Microbes producing bioplastics

Extensive research on microbial bioplastics has revealed that diverse microorganisms produce and store PHAs/PHBs as sources of carbon and ATP. The type and molecular masses of the polymers produced varied with different microbes, carbon sources, and growth parameters (Albuquerque et al., 2011). Several bacterial strains such as Bacillus*, Pseudomonas, Citrobacter, Enterobacter, Escherichia and Klebsiella* are some of the most well-known PHA/PHB producing bacteria. In addition, the production of PHB is also evident in microbial members involved in the nitrogen cycle, for example, *Rhizobium leguminosarum*, *R. hedysarum, R. galegae, A. macrocytogens, Azotobacter beijerinckii,* and *A. vinelandii*, undermining that PHB also influences their growth (Bhatia et al., 2018; Patel and Parsania, 2018; Moreno-Bayona et al., 2019; Chozhavendhan et al., 2020).

Bacteria are classified into two types based on the culture conditions that promote PHA accumulation: (1) bacteria that require an abundance of carbon and limit critical nutrients (such as oxygen and nitrogen) for many PHA syntheses. Examples include *Protomonas extorquens*, *P. oleovorans,* and *Cupriavidus necator.* (2) Bacteria that do not require nutrient restrictions can produce PHA during the log phase, e.g, *Azotobacter vinelandii* and *Alcaligenes latus* (Albuquerque et al., 2011). The cultivation condition of PHA biosynthesis is a necessary prerequisite for the large-scale production of PHA. Furthermore, it was shown that

methylotrophic bacteria generate PHB, though in low quantities (Suzuki et al., 1986). Additionally, another category of PHA producers from bacterial domains requiring moderate salt concentrations belongs to the Halomonadaceae family; for instance, *Halomonas* sp. synthesizes small chain length (scl)-PHA. Lower NaCl (3–15%) is a prerequisite for the optimal growth of most *Halomonas* species. Kawata and Aiba (2010) have reported that, *Halomonas*sp. KM-1 could produce PHB using glycerol as the sole carbon source. Furthermore, it has been reported that cyanobacteria with PHA synthase enzymes accumulate PHA by utilizing CO2 and sunlight. Low molecular weights PHB are also reported in yeast and other eukaryotic bacteria which use polyphosphate complexes in membrane transport. These include *Saccharomyces cerevisiae, Candida krusei, S. diastaticus, Kloeckera apiculata, C. tropicalis, Rhodotorula glutinis, Kluyveromyces Africans, K. lactis* and *Ralstonia eutropha* (Portugal-Nunes et al., 2017; Soto et al., 2019). Also, recently it was reported that *Bacillus* sp. can be used for the fermentation and bioplastic production from medical plant waste and waste frying oil (Mahari et al., 2022). Licciardello et al. (2019) reported that *Pseudomoas corrugate, Pseudomonas mediterranea* can produce medium chain length PHA. *Cupriavidus necator* can synthesize PHA by using volatile fatty acids (Al-Battashi et al. 2020). An overview of various microorganisms producing different types of bioplastics is summarized in Table 1.

3.2. Algal production of bioplastics

Production of bioplastics is not only confined to microbes, algae can also be used for the production of bioplastics. Starch, PHA, Cellulose, PLA, PVC, PE and some protein-based polymers are currently reported to be derived from algal biomass. Algal bioplastic production has some advantages such as alleviating greenhouse effect by absorbing carbon dioxide, enhancement of plastic quality as well as ability to be grown in large quantity in less place (Zhang et al., 2019a, b; Shi et al., 2012; Beckstrom et al., 2020). Moreover, the use of algae for bioplastic production nullifies the concern of using human food source or waste as fermentation media, when the resources to meet food demands are meagre. Bioplastic production of algae can be done by using algal biomass directly, blending algae with other materials, intermediate biorefinery processing and application of genetic engineering for improved bioplastic production (Rahman and Miller, 2017). *Cholrella* sp. (Otsuki et al., 2004), *Ulva armoricana* (Chiellini et al., 2008), *Spirulina* sp. (Zeller et al., 2013), *Laminaria japonica, Enteromorpha crinite* (Jang et al., 2013) etc, are some of the reported algal species used for bioplastic production.

The bioplastic synthesis pathway, especially of PHA, is well documented in cyanobacteria. Adequate amount of carbon source but insufficient nitrogen and phosphorous favours the biosynthesis of PHA and its accumulation in the cells. Acetyl-CoA produced during the normal biochemical reaction in the cells under appropriate condition is used to form PHA. Biosynthesis of PHA involves three enzyme involved steps (i) condensation of acetyl-CoA to form acetoacetyl-CoA by β-ketothiolase (ii) reduction of acetoacetyl-CoA to hydroxybutyryl-CoA by acetoacetyl-CoA reductase (iii) esterification of hydroxybutyryl-CoA to PHA by PHA synthase (Mal et al., 2022).

Various biopolymers derived from algae are the best candidates for bioplastic production. The highlight of using microalgae for bioplastic production is its cost-effectiveness. Microbial production of bioplastics needs large quantities of substrates when compared to production using microalgae because algae are auto-tropic. They use CO2 and light for their food, thereby reducing the cost of providing substrates. Moreover, using algae for bioplastic production shows more inclination toward a circular bio-economy as they have features such as low cost, low CO2 generation and low greenhouse gas emission etc (Dang et al., 2022).

Cyanobacteria such as Synechococcus sp. (Nishioka et al., 2001), Synechocystis sp. (Panda and Mallick, 2007), and Muscorum sp. (Sharma and Mallick, 2005) can produce 30–80% of PHB. *Chlorella* sp. are the best candidates for making starch-based bioplastics and biobased polymer blends such as blends with polyvinyl alcohol, PE and glycerol. *Spirulina* sp. is also an ideal candidate for biobased blends and bioplastic production (Onen Cinar et al., 2020). Another microalgal species known to produce PHA is Calothrix scytonemicola (Johnsson and Steuer, 2018). Bioplastic production is also exhibited by some macroalgal species. Macroalgae can also be employed as a feedstock for the production of bioplastics. Also, some of the derivatives from the macroalgae can be exploited for the production of bioplastics. Mainly carrageenan, which can be obtained from marine macroalgae such as Kappaphycus sp. and alginates that can be obtained from Macrocystis sp. can be used. Those derivatives can be used to make blends with glycerol and polyvinyl alcohol to manufacture biodegradable plastic films (Dang et al., 2022).

4. Molecular basis of bioplastic production

In the past two decades, some scientific discoveries focused on the biosynthesis of biopolymers have proved that microorganisms capable of synthesizing bioplastics undergo different metabolic pathways according to the type of the medium components (Fig. 1) (Simó-Cabrera et al., 2021). However, acetyl-CoA is the initial metabolite described among the three notable routes followed by microorganisms. When carbohydrate is the primary source in the culture media, it is metabolized to pyruvate, ultimately used to synthesize PHAs (González García et al., 2013). In comparison with plants [<10% (w/w)], bacteria accumulate PHAs up to 90% (w/w) of the microbial dry weight (Verlinden et al., 2007).

Cytosol based PHA synthase initiates PHA accumulation using acetyl CoA monomeric units. The PHA biosynthesis pathway comprises three distinct enzymatic reactions. In the first step, β-ketoacylCoA thiolase (*phbA*) catalyzes the condensation of two acetyl-coenzyme A (acetyl-CoA) molecules into acetoacetyl-CoA. Secondly, a reduction of the latter product to (R)-3-hydroxybutyryl-CoA occurs by acetoacetyl-CoA dehydrogenase/reductase (*phbB*). Finally, the polymerization of monomers to PHB is catalyzed by the polymerase (*phbC*) (Shabina et al., 2015). Microbes can initiate PHB synthesis from sugars and fatty acids following the beta-oxidation pathway and the de novo fatty acid biosynthetic pathway, as noted in Fig. 1. The various intermediates of fatty acid metabolism are eventually converted to (R)-3-hydroxyacyl-CoA, and corresponding (R)-3- hydroxy fatty acids are produced, which are further polymerized to form PHA. Once the oxidation of carbon is done, the intermediates in de novo fatty acid biosynthesis will divert to PHA biosynthesis, which is catalyzed by transacylase (*PhaG*). The oxidation of enoyl-CoAto (R)-3-hydroxyacyl-CoA is catalyzed by enoyl-CoA hydratase (PhaJ) and further to PHA by PHA synthase enzymes (*PhaC*) (Yadav et al., 2019).PHA/PHB polymers accumulate primarily in the form of granules within the bacteria due to their hydrophobicity. These accumulated granules comprise polymerized PHAs moieties associated with phospholipids and bacterial cells called phasins. Such molecular entities make PHAs a more stable crystalline polymer that prevents them from interacting with water within the bacterial cells. The presence of phasins on the hydrophobic core aids in the identification of the PHA granule's number and size (Pötter et al., 2002).

5. Advancements in the methodologies used for enhanced bioplastic production

Bioplastics are produced on a large scale by various processes, depending on their advantages and disadvantages, followed by a subsequent selection of the best ones. To enhance its productivity and bring down its production costs, international interests in developing novel methods for bioplastic production are inflating. In this context, the shortcomings of the old ways are processed and modernized so that the advanced techniques become more successful. Fig. 2 outlines the main strategies adopted to improve bioplastic production.

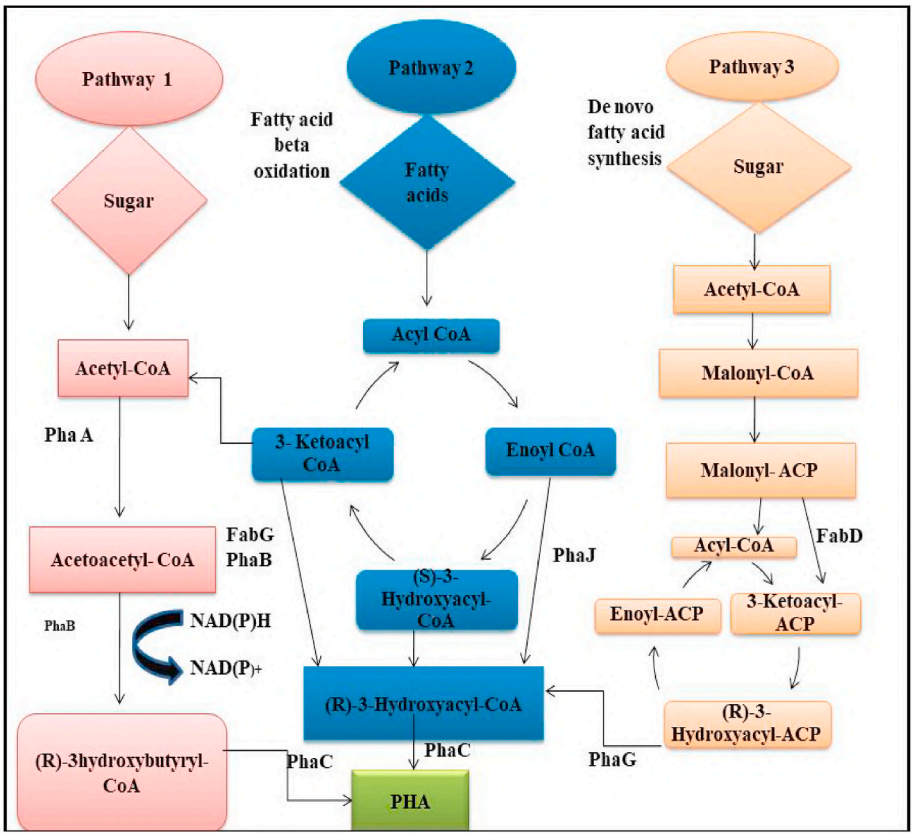

Fig. 1. The metabolic pathways responsible for PHA production (PhaA: b-ketothiolase; PhaB: acetoacetyl coenzyme A(CoA) reductase; PhaC: PHA synthase; FabG: 3-ketoacyl acyl carrier protein (ACP) reductase; PhaG: acyl-ACP-CoA transacylase; PhaJ: enoyl-C ketoacyl acyl carrier protein (ACP) reductase; PhaG: acyl-ACP-CoA transacylase; PhaJ: enoyl-C) (Adapted from Khatami et al., 2021).

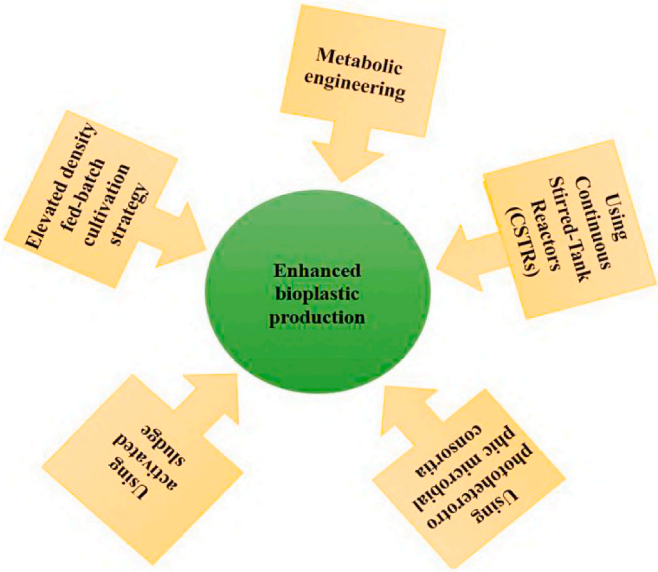

Fig. 2. Strategies for enhanced bioplastic production.

5.1. Elevated density fed-batch cultivation strategy

The development of enhanced fermentation technology accelerating scaling up can serve microorganisms as an ideal source for synthesizing recognized and novel microbial products (Varghese et al., 2021). To achieve higher concentrations of the product in the medium, high-density cultivation is developed by growing cells in elevated densities. This strategy is considered an effective tool in modern bioprocessing (Subramaniam et al., 2018). The fermentation process involved in PHA production is generally challenging and is controlled through two or more fermentation stages to meet a higher polymer yield. The use of extremophilic microorganisms is advantageous, and they have a considerable effect against contamination; hence fewer sterility precautions have to be taken. Various factors such as bacterial biomass (74–92%), high monomer content (92–99%), feeding modes (pulse, constant, mixed) as well as culturing methods such as fed-batch greatly influence the extent of PHA production (Huong et al., 2017). Norhafini et al. (2019) have proposed that a minimum level of nitrogen supplementation should be maintained to aid microbial growth and subsequent PHA accumulation. Moreover, it's noted that fed-batch fermentation offers excellent control to prevent complete loss of medium carbon and nitrogen and dramatically affects the polymer's properties and productivity, making it highly recommended for PHA production.

5.2. Using activated sludge for the enrichment and PHAs production

The process of wastewater treatment results in the formation of activated sludge. Since the usage of activated sludge does not demand sterilization conditions that further reduce the PHA production costs, it is considered an excellent replacement for pure bacterial strains (Valentino et al., 2015). Several studies have succeeded in activating sludge to enrich PHAs on a laboratory scale under artificial conditions. These investigations focused on upgrading the PHA production capacity of activated sludge.

Several research investigations have been carried out on the optimization studies for activated sludge, such as pH, oxygen concentration, addition or reduction of nutrients and organic substrates, solid retention

time, feeding methods, etc. (Chen et al., 2013; Bassi et al., 2021). The extracellular polymeric substance (EPS) of activated sludge maintains its chemical properties and microbial flocculation and plays a crucial role in PHA production. This works in two perspectives: (1) in the early stages, accumulated PHAs oppose EPS accumulations, (2) at the final reaction phase, when carbon sources are deprived, PHA accumulation uses energy for EPS. EPS production and consumed sludge properties fluctuate wildly during these reaction stages, and in the subsequent course, most PHAs are synthesized in the microbial cells. Furthermore, the structure of sludge flocs influences solid-liquid separation and the reaction rate. This reverses the efficiency and cost of PHA production (Cui et al., 2017).

Physicochemical properties of the sludge, such as biomass concentration, affect PHA accumulation (Sakai et al., 2015). Conversely, it is necessary to examine other parameters such as pH, temperature and aeration during PHA production to develop successful methodologies. Li et al. (2019) operated batch reactors that used mixed carbons for PHB production and discovered that although sludge floc size had a negative impact on PHAs accumulation, Mixed Liquor Suspended Solids (MLSS)/polysaccharides had a positive impact on the formation of PHAs. Irrespective of the fact that sludge is converted into useful bioplastic, lack of cost effectiveness, inconsistency in sludge composition and need for constant optimization is a major challenge in us of activated sludge for bioplastic production at industrial levels.

5.3. Using photoheterotrophic microbes

Photoheterotrophic microbes utilize different metabolic pathways in response to various substrates, predominantly using acetate and butyrate to produce PHA in pure or microbial consortiums (Reddy et al., 2014). Reports have suggested that microbial consortia produced PHA yields of most total suspended solids (TSS) (Bhalerao et al., 2020) comparatively higher than pure culture production. Tables 2 and 3 illustrate a comparison study of microbial consortia and pure cultures used for optimum production of bioplastics. The composition of the substrate leads to several quantities of monomers in polyhydroxybutyrate (PHB) and polyhydroxyvalerate (PHV) copolymers (Villano et al., 2010). The properties of these copolymers can be subsequently changed to a great extent as a unit of a 3-hydroxyvalerate (3HV) monomer. There are distinct strategies to reduce costs by optimizing the fermentation conditions and increasing production efficiency (Dietrich et al., 2017). Albuquerque et al. (2013) noted that *Paracoccus* sp. from a microbial consortium utilized a higher proportion of butyrate and propionate than valerate and acetate, while *Thauera* and *Azoarcus* preferred butyrate and acetate, respectively, contributing to a sustained high PHA production.Moreover, it was observed that during PHA production, mixed cultures of photosynthetic bacteria utilized acetate as a co-substrate for the assimilation of butyrate and propionate. However, another study (Liu et al., 2011) discovered higher concentrations of PHB accumulating microorganisms in activated sludge accustomed to a single carbon source. So, to generalize, the microbial carbon dependence on bioplastic production is not acceptable. Photoheterotrophic bacteria such as *Pseudomonas*, *Rhodopseudomonas* and *Clostridium* could use acetate and butyrate separately and in a mixture for PHA production (Guerra-Blanco et al., 2018), though butyrate consumption was lesser than acetate. However, the growth rates and the substrate consumption of acetate in a mixture were almost the same.

5.4. Using continuous stirred-tank reactors (CSTRs)

Since continuous microbial enrichment cultures obliterate sterile fermentation conditions, usage of organic waste as a substrate is highly recommended (Chen, 2009). For example, fermented waste streams obtained from the food and paper industries could be used as substrates for microbial enrichment cultures producing PHAs that would remarkably reduce their costs and further permit a wide array of applications (Albuquerque et al., 2011). The PHA production process could be modified by combining the feast-famine conditions in two continuous stirred tank reactors (CSTRs) with partial biomass recycling (Marang et al., 2015). This 2-stage system has a constant feed power supply with spatially separate feast and famine phases. However, since the first reactor receives the oversupply of substrates under the feast conditions, only trace amounts will end up in the (second) famine reactor. Therefore, these conditions can cause selection pressure on PHA accumulating bacteria by influencing their affinity towards the substrate and bacteria's maximal substrate uptake rate (Amulya et al., 2015).

Previous experimental studies by Bengtsson et al. (2008) and Albuquerque et al. (2011), who used a 2-stage CSTR system to enrich PHA-producing bacteria, did not respond to the influence of the chosen reactor configuration on the microbial competition. Marang et al. (2018) have demonstrated the effect of continuous acetate feeding while enriching PHA producing bacteria in 2-SBRs. In addition to enriched

Table 2
Productivity of bioplastics by pure cultures at the laboratory scale.

Sl. No.	Microorganisms	Carbon source	Type of Bioplastics	Content (%)	References
1	*Bacillus megaterium* UMTKB-1	Medical plastic waste + Waste frying oil (800 W)	P(3HB)	1.54 ± 0.13	Mahari et al. (2022)
2	*B. gladioli* 2S4R1	Glucose + Xylose + Arabinose	PHB	52.06	Naitam et al. (2022)
3	*B. cereus* LB7	Glucose + Xylose + Arabinose	PHB	50.71	Naitam et al. (2022)
4	*L. mesenteroides*	Cheese whey	PHA	36	Bosco et al. (2021)
5	*Cupriavidus necator*	Volatile fatty acids from paper wastes	PHA	60.71	Al Battashi et al. (2021)
6	*Cupriavidus necator*	Cheese whey	3HB 3HV	71	Domingos et al. (2018)
7	*Cupriavidus necator*	Waste rapeseed oil	3HB 3HV	76	Obruca et al. (2010)
8	*Bacillus megaterium*	Sucrose	3HB	62	Faccin et al. (2013)
9	*Pandoraea* sp. MA03	Crude glycerol	3HB	49	de Paula et al. (2017)
10	*Pseudomonas aeruginosa* ATCC 27,853	Long odd chain fatty acids (heptadecanoic acid, nonadecanoic acid, heneicosanoic acid)	3HB 3HV	13.4	Impallomeni et al. (2018)
11	*Pseudomonas putida*	Glucose + glycerol + octanoate	HHx, HO, HD	57	Fontaine et al. (2017)
12	Recombinant *Pseudomonas putida*	Waste vegetable oil	HHx, HO, HD	38.3 ± 3.1	Borrero-de Acuña et al. (2019)
13	*Burkholderia sacchari*	Waste paper	PHB	44.2	Al-Battashi et al. (2019)
14	*Burkholderia sacchari*	Glucose + different co-substrates	PHB	2.7–73.7	Mendonça et al. (2014)
15	*Bacillus* sp. ISTVK1	Pure glycerol	PHV	85.19	Morya et al. (2018)

Table 3
Productivity of bioplastics by mixed cultures at the laboratory and pilot scale.

Sl. No.	Microorganisms	Carbon source	Type of Bioplastics	Content (%)	References
1	*Bacillus megaterium* UMTKB-1	Medical plastic waste + Waste frying oil (800 W)	P(3HB)	1.54 ± 0.13	Mahari et al. (2022)
2	*B. gladioli* 2S4R1	Glucose + Xylose + Arabinose	PHB	52.06	Naitam et al. (2022)
3	*B. cereus* LB7	Glucose + Xylose + Arabinose	PHB	50.71	Naitam et al. (2022)
4	*L. mesenteroides*	Cheese whey	PHA	36	Bosco et al. (2021)
5	*Cupriavidus necator*	Volatile fatty acids from paper wastes	PHA	60.71	Al Battashi et al., (2021)
6	*Cupriavidus necator*	Cheese whey	3HB 3HV	71	Domingos et al. (2018)
7	*Cupriavidus necator*	Waste rapeseed oil	3HB 3HV	76	Obruca et al. (2010)
8	*Bacillus megaterium*	Sucrose	3HB	62	Faccin et al. (2013)
9	*Pandoraea* sp. MA03	Crude glycerol	3HB	49	de Paula et al. (2017)
10	*Pseudomonas aeruginosa* ATCC 27853	Long odd chain fatty acids (heptadecanoic acid, nonadecanoic acid, heneicosanoic acid)	3HB 3HV	13.4	Impallomeni et al. (2018)
11	*Pseudomonas putida*	Glucose + glycerol + octanoate	HHx, HO, HD	57	Fontaine et al. (2017)
12	Recombinant *Pseudomonas putida*	Waste vegetable oil	HHx, HO, HD	38.3 ± 3.1	Borrero-de Acuña et al. (2019)
13	*Burkholderia sacchari*	Waste paper	PHB	44.2	Al-Battashi et al. (2019)
14	*Burkholderia sacchari*	Glucose + different co-substrates	PHB	2.7–73.7	Mendonça et al. (2014)
15	*Bacillus* sp. ISTVK1	Pure glycerol	PHV	85.19	Morya et al. (2018)

Zoogloea sp., acetate was continuously added to the first reactor; however, enrichment cultures on an SBR dominated by *Plasticicumulans acidivorans* gave a five-fold yield.

5.5. Metabolic engineering

Strain improvement and metabolic engineering procedures have been widely applied with the primary objective of making bioplastic production more efficient and competitive. These advanced technologies have allowed PHA producers to improve their cultivation parameters. Furthermore, metabolic engineering has also been used to refine the quality of PHAs by modifying their chemical properties like monomer composition, chain length and molecular weight (Agnew and Pfleger, 2013; Wainaina et al., 2020a; Liu et al., 2021a).

5.5.1. Expanding substrate utilization

According to Ren et al. (2018), metabolic engineering can be utilized to accelerate the growth of a PHA producer. Jarmander et al. (2015) depicted that during the production of a PHB monomer (R) 3-hydroxybutyrate, the recombinant strain could simultaneously uptake xylose, arabinose and glucose by eliminating the *pts* G-gene and allowing it to evolve in arabinose. Thus, expanding substrate utilization also positively influences PHA production.

5.5.2. Engineering cell morphology

Along with significant microbial growth rate and rapid carbon source utilization, the design of cell morphology is also a critical factor in enhancing the accumulation of PHA. Controlled gene expression will cause changes in the cell's morphology such as length and size of the cells especially. Larger cell size will help cells to harbour more amount of substrate for PHA production and as a result PHA production will also increase (Zhao et al., 2019). For example, using CRISPRi, *Halomonas* TD01 was constructed to suppress the expression of the *FtsZ* gene, resulting in filamentous cells with higher levels of PHA (Tao et al., 2017). Wang et al. (2014) have also demonstrated the overexpression of *the sul*A gene by a recombinant PHA producer, *E. coli,* by modifying its cell morphology, caused a double increase in PHB content.

5.5.3. Optimizing metabolic-pathways

Optimizing the metabolic pathways is another trend followed during metabolic engineering. While pathway optimization, the main objective must be to attain higher expression levels of PHA enzymes for rapid polymer synthesis. The formation of intermediates or metabolic stress within the cell must be avoided. Another strategy to optimize the pathway is by modifying the PHA enzyme's promoter strength (Shen et al., 2018; Liu et al., 2021b) by site-directed mutagenesis or codon optimization to increase the enzyme activity (Zhang et al., 2019a, b; Wainaina et al., 2020b), by eliminating competitive pathways that reduce PHA contents or by allowing heterologous expressions of different microbial enzymes. In the PHA pathway, one of the predominant competitive reactions is the degradation of the polymer, which is catalyzed by endogenous PHA depolymerase (*phaZ*). Studies carried out by Cai et al. (2009) have proven that PHA accumulation by *P. putida* could be improved from 66 to 86 wt% of its cell's dry weight by deleting the *phaZ* gene. Though *E. coli* lacks the *phaZ* gene, acetate formation by it is considered the crucial competitive pathway during PHAs production. To eliminate such competitive pathways, several research on metabolic strategies to subdue it and further escalate their titer, product rate, and yield have been reported (Perez-Zabaleta et al., 2019; Zhuang and Qi, 2019). Recombinant *E. coli* which could produce lower amounts of acetate could produce 2–3fold greater levels of (R)-3-hydroxybutyrate) (Perez-Zabaleta et al., 2019).

5.5.4. Increasing precursor availability

Another approach to redirect the flux toward product formation is to intensify the precursor's availability, mainly Acetyl-CoA, common in most PHA pathways (Fig. 1). Acetyl-CoA's accessibility can be elevated by overexpression of genes responsible for PHA production or by developing alternate pathways such as SACA pathway (Synthetic Acetyl-CoA). According to Lu et al. (2019), SACA pathway is a conserved carbon pathway independent of ATP, which produces Acetyl-CoA using a sole carbon source in a three-step reaction process. Anfelt et al. (2015) have reported that the overexpression of phosphoketolase could inflate acetyl-CoA's availability to six-folds and increase PHA synthesis.

5.5.5. Cofactor availability

The availability and regeneration of cofactors are essential factors in PHA production since the second step requires NADPH as a cofactor. The reductase of most PHA-producing microorganisms uses NADPH as a necessary cofactor except for those of *Chromatium vinosum* (dependent on NADH) (Liebergesell and Steinbuchel, 1992) and of *Halomonas boliviensis* reductase (utilizes both cofactors, but preferably NADPH) (Perez-Zabaleta et al., 2016). Improving the ability to conserve NADPH through overexpression of glucose phosphate dehydrogenase (zwf) has promoted the yield of PHB (Lim et al., 2002) and (R)3-hydroxybutyrate (Perez-Zabaleta et al., 2016). The overexpression of NADkinase led to an increased supply of NADPH which further improved the PHB yield to 76%. Alternatively, the insertion of enzymes such as ribulose-1, 5-bisphosphate carboxylase/oxygenase (RuBisCo) and phosphoribulokinase into the PHA pathway allowed excess NADH to be reused,

further increasing the yield of the product on sugars (Li et al., 2009).

5.6. rDNA technologies

At present, rDNA technologies have gained significant importance in achieving the desired cell function of an organism through random mutagenesis or adaptive evolution, leading to altered variations in their phenotypes and metabolic pathways. Snell et al. (2002) have proven this revelation through their research which suggested that reverse engineering of YfcX (3-hydroxyacyl-CoA dehydrogenase) has been significant in mcl-PHAs synthesis. Pries et al. (1990) have reported that *Pseudomonas saccharophila* and *Cupriavidus necator* were genetically modified to utilize lactose and galactose through reverse engineering. However, they synthesized lower amounts of PHB. Lactose conversion was achieved by introducing the genes *lacZ* (encoding for β-galactosidase), *lacO* (the lac operator), and *lacI* (encoding for a lac repressor) of *E. coli*. By one-step conversion, the resulting recombinant strains produced PHAs from lactose. The strategy followed by the authors was to insert the lac operon into one of the depolymerase genes (phaZ1) to reduce polymer depolymerization by the cell and ultimately increase the yield of PHA production. The switching off of *the phaZ1* gene led to a 30–40% less depolymerization even without a carbon source (Povolo et al., 2010). Likewise, several genetic modifications were carried out in microbes to impart improved PHA yield by using different types of waste as carbon sources in Table 4.

6. Pioneering applications of bioplastics

Bioplastics have been applied in several fields, including industrial, agricultural, and medical applications, with proven consistency. Fig. 3 illustrates the pioneering applications of these biopolymers.

6.1. Industrial applications

PHB can be used to make heteropolymers by moulding, extruding, spinning into fibres and processing into food packaging films. As compared to the conventional packaging material, these films were distinguished by excellent oxygen permeability (OP), considerable tensile strength, high antioxidant activity, high water vapour transmission rate (WVTR) and significant antimicrobial action (Ma et al., 2018).

PHAs are relatively expensive to manufacture; plastics are incorporated with inert fillers or additives, such as clay minerals and wood flour, to lessen manufacturing costs. The use of biorefinery lignin residue extracted from corn stalks mixed with P(3HB-co-4HB), bagasse based soda lignin, and PHB mixed with biorefinery lignin residues derived from *Arundo donax* are some examples (Angelini et al., 2016). Augmentations in the PHB-lignin composites properties during 3D printing were recently demonstrated (Sutton et al., 2018). Pinus-based biorefinery lignin in PHB composites, processed into films, is effectively used in 3D printing (Vaidya et al., 2019).

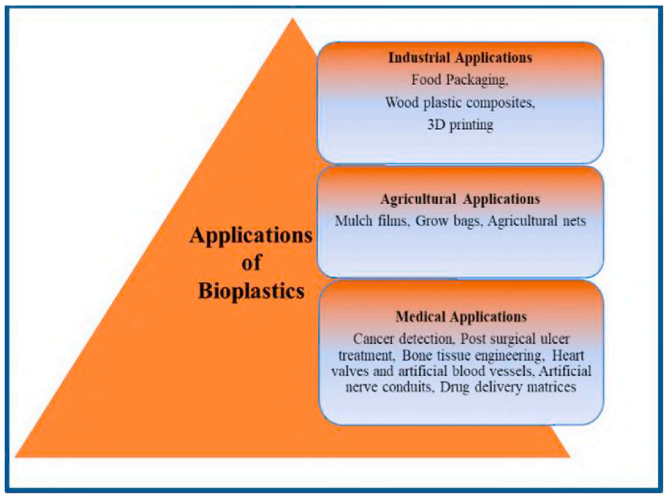

Fig. 3. Pioneering applications of bioplastics.

6.2. Agricultural applications

The applications of bioplastics in agriculture are pretty limited. So far, agricultural uses such as grow bags, farm nets and mulch films have been studied. Agricultural nets made up of biodegradable PHAs are being considered at the moment. The compostability of PHA's biodegradable meshes allows the bioplastic to be disposed of directly into the soil. Different bioplastics such as PHB and their blends with PLA are most widely used for manufacturing agricultural nets due to their high tensile strength (Kusuktham and Teeranachaideekul, 2014). Production of PHA-based grow bags sequesters nitrogen from the water, does not pollute the surrounding water bodies, prevents root reformation, and avoids pollution concerns (Adane and Muleta, 2011). Agricultural mulch films are critical for increased crop yield and protection, apart from grow bags. Mulch films can retain moisture content, maintain excellent soil structure and prevent contamination by managing nuisance weeds and it is noted that plastic mulch accounts for 40% of agricultural mulch (Rydz et al., 2015). High density polyethylene

Table 4
List of genetically modified microbes used for enhanced PHA production by using different types of waste as carbon source.

Sl.. No.	Microorganisms involved	Genetic modifications done	Type of waste used as carbon source	References
1.	*R. eutropha (C. necator)*	*Mannheimia succiniciproducens* MBEL55E *sacC* gene	Molasses	Park et al. (2015)
2.	Modified *C. necator H16*	Sucrose utilization (*csc*) genes of *E. coli*		Arikawa et al. (2017)
3.	*C. necator* mutant	*Aeromonas caviae* PHA-synthase gene	Waste lipids	Fukui and Doi (1998)
4.	*Pseudomonas putida*	*Pseudomonas* lipase genes		Solaiman et al. (2001)
5.	*P. oleovorans*			
6.	*Bacillus licheniformis*	Sequential mutations		Sangkharak and Prasertsan (2013)
7.	*Escherichia coli*	Endoxylanase (XylB) from *S. coelicolor* and a β-xylosidase (XynB) from *B. subtilis*	Cellulosic materials	Salamanca-Cardona et al. (2014)
8.	*Rhodospirillum rubrum*	PHA synthase genes (*phaC*)	Syngas	Klask et al. (2015)
9.	*Escherichia coli*	Addition of *C. butyricum's* glycerol dehydratase genes; *Salmonella enterica's* propionaldehyde dehydrogenase, and *R. eutropha's* (*C. necator*) PHA synthase gene	Crude glycerol	Andreeβen et al. (2010)
10.	*Escherichia coli*	Phosphotransferase system mutant	Lignocellulose hydrolysates	Li et al., 2007a, b
11.	*Aeromonas* sp.	inserting the operon of *C. necator* (*phaCAB*)	Starch	Chien and Ho (2008)

(HDPE), low density polyethylene (LDPE), and linear LDPE are generally used to synthesize plastic mulch. As a result, they frequently end up in landfills or get incinerated, which further causes environmental pollution. In recent years, studies on bioplastics such as polybutylene succinate, PLA, corn starch polymers, ethylene vinyl acetate and other PHAs have been reported (Niaounakis, 2015; Wainaina et al., 2019). Further research on the extensive usage of bioplastics for mulch production can validate them as a sustainable alternative to traditional plastic mulch films.

6.3. Medical applications

PHAs' biocompatibility makes them an essential compound for medical applications. They serve as biomaterials while directing medical therapy by eliciting an acceptable host response. PHAs have been applied in tissue engineering in some medical techniques, including injection, plates, pins and fracture fixation devices. In 2007, Food and Drug Administration (FDA) suggested that PHA uses in biomedical domains would have a bright future. Sabarinathan et al. (2018) reported the inherent biocompatible nature of PHB through its application in cancer detection as cancer cells adhered firmly to PHB sheets, whereas normal cells did not.PHA based implants of heart valves, drug delivery agents, tissue engineering of nervous, vascular and orthopaedic tissues are yet some successful usages of bioplastics in medicine. Furthermore, long-term implantation of PHAs has been non-carcinogenic (Lizarraga-Valderrama et al., 2015; Panith et al., 2016).

Bioplastics, mainly poly (3 hydroxybutyrate co 3 hydroxyhexanoate) PHBHHx, exhibit a positive role in promoting bone tissue growth, while hydroxyapatite (HAP) mixed with PHB displayed improvements in the modulus of elasticity in compression, and cell division (Sadat-Shojai et al., 2016). The biocompatibility and elasticity of P3HB4HB enable elastin-based artificial blood vessels, whereas P3HB4HB-diol shows low platelet adhesion (Li et al., 2011). Intriguingly, PHB has been beneficial and applicable in the neurological fields. It has been reported to help the survival, multiplication and attachment of the adult Schwann cells along neural axons. PHB tubes could enhance common perennial nerve injury for peripheral nerve regeneration, and PHBHHx promotes neural repair (Novikova et al., 2008). Interestingly, hydrophobic PHA nanoparticles, engineered PHA synthase system fused PHB nanoparticles in addition to colon cancer are ideal for ideal drug delivery agents (Panith et al., 2016). Moreover, Chaturvedi et al. (2015) could successfully load an insulin delivery system mixed with PHBHHx nanoparticulate phospholipids (INSPEC-NPs), which exhibited an extended therapeutic effect. Similarly, PHB/Polyethylene glycol (PHB PEG) nanoparticles have been proven to achieve insulin encapsulation and maintain its release (Chaturvedi et al., 2015).

7. Major bottlenecks and future perspectives of bioplastic production

Bioplastics have transformed into an inventive research area for scientists around the world. The necessity for eco-friendly alternatives has resulted in this progressive development (Shamsuddin et al., 2017). This field has developed very dynamically since introducing the first modern biological plastics some 30 years ago. The introduction of bioplastics can certainly bring risks and benefits, but the truth is that they are essential to replace currently used plastics. The potentiality of every biochemical process is assessed depending on its performance, product titre, production rate, post-processing efficiency, and cost concerns (Noorman and Heijnen, 2017). When compared to ordinary polymers, PHAs have higher production costs. Several challenges must be conquered to reduce their manufacturing costs and make PHAs economically viable. The choice of raw materials is the most critical challenge to consider as substrate costs typically represent40-60% of total biobased product costs. The overall throughput of bioplastics production is significantly lower than that of similar petroleum-based plastic production. Utilizing less expensive substrates and their availability throughout the year is critical for commercializing PHA synthesis. The logistics of collecting and transporting the raw material can also generate some costs. One proposed option is to integrate PHA synthesis into existing industrial plants and transform them into multi-production biorefineries by utilizing industrial wastes, thereby providing a continuous substrate for PHA production by reusing and recycling trash (Nguyen et al., 2018).In the meantime, in regions like South America and Asia, large-scale production capacities are increasingly installed where low-cost feedstocks, e.g. sugarcane and molasses, are available in sufficient quantities (Storz and Vorlop, 2013).

Biopolymers' future market is anticipated to escalate due to their sustainability. With the aid of biotechnologically proven advanced methodologies, the usage of microorganisms could remarkably influence PHA production to conquer current challenges. Due to their similar properties and incredible features, such as biocompatibility and biodegradability, microbial PHAs are ideal alternatives to routinely used petro-plastics. Nevertheless, there are critical limitations to the mass production of bioplastics using microbes (Francis et al., 2021). Setbacks related to downstream processing, a low substrate to product conversion ratio, and irregularities in bioplastic properties of each batch are some of the blocks faced during PHA commercialization. Recombinant organisms producing bioplastics using cheaper carbon sources such as lactose, glycerol, molasses, sucrose, oils and methane can be constructed by exploring the microbial biosynthetic pathways and their regulatory pathways (Madison and Huisman, 1999; Poirier, 2002). In the case of mixed cultures, the application of bioaugmentation strategies to bring a substantial productive yield should be investigated. The biomass bioaugmentation of *Plasticicumulans acidivorans* resulted in 85%PHB accumulation from mixed culture processes (Marang et al., 2018), whose output was higher than an individual culture. Such mixed cultures can lead to the substantial conversion of the raw materials with inflated biopolymer formation, further bringing the commercial PHA production closer to reality.

A significant extent of the total cost of PHA production is to extract bioplastics. Using more economical and sustainable methods to recover PHAs will considerably deduct the total cost of PHA production.PHA extraction methods include digestion, solvent extraction, and floatation, which consume large quantities of chemicals and result in associated expenses. Due to chlorinated solvents or surfactants, PHA production is estimated to be approximately thrice more expensive than petrochemically derived plastics (Sun et al., 2007). Research that focuses on using more economical and eco-friendly chemicals and solvents is critical. Another bottleneck that has to be addressed is improving the recovery efficiency. Research on morphology engineering, which can alter the size and form of PHA granules, is critical for optimal downstream processing. The discovery of mechanisms that allow PHAs to accumulate extracellularly can bring up a novel window of research opportunities. The extent of bioplastic accumulation could be thus being increased, recovery would be easy, and a new pace of production could be generated by extracellular bioplastic accumulation (Khatami et al., 2021). Therefore, the future of bioplastics is believed to depend on the efforts made to fulfil reasonable costs and performance yield.

When we talk about the environmental impact of bioplastics it stands as a controversy. But the harmful effects of bioplastics are less when compared to the conventional petroleum-based plastics. In composting conditions decomposition of bioplastics will produce methane. So, during massive composting of bioplastics in landfill sites may contribute to global warming. The main priority of growing maize and corn which can be used for bioplastic production will shift from food security to bioplastic production. This will compete with food production and security. Chemical pesticides used in these crops will also pollution on other side. Also, chemicals used for converting the organic material to bioplastic will cause issues when they released to the environment (Atiwesh et al., 2021).

8. Conclusion

This review uncovers recent advances in microbial production of bioplastics. Microbial bioplastics are considered sustainable alternatives to conventional plastics. Diverse microorganisms synthesizing different types of bioplastics have been described here. Detailed research on the molecular basis of bioplastic production revealed that various metabolic pathways are responsible for synthesizing biopolymers depending on the available substrate in the growth medium. This review article also illustrates the implementation of advanced methodologies for microbial bioplastic production such as various advanced fermentation processes, metabolic engineering, engineering cell morphology, genetic engineering that promote bioplastic production and sustainability. Due to their predominant biocompatible traits and novel applications, we may conclude that microbial bioplastics have a promising future. Apart from the beneficiary traits bioplastics also can cause some environmental issues, but those were less harmful when compared to the petroleum-based plastics.

Credit author statement

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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

Data will be made available on request.

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