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Review

Valorisation of Sugarcane Bagasse for the Sustainable Production of Polyhydroxyalkanoates

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Abstract: With the world shifting towards renewable and sustainable resources, polyhydroxyalkanoates (PHAs) have attracted significant interest as an alternative to synthetic plastics. While possessing promising properties suitable for various applications, the production of PHAs has not yet reached a global commercial scale. The main reason is the high cost of production, which represents a major limitation. Sugarcane bagasse (SCB) is an abundant lignocellulosic waste around the world. Its use to produce PHA enhances the feasibility of producing PHAs at commercial scale. However, SCB requires pretreatment and hydrolysis steps to release the sugars prior to the microbial fermentation. The cost associated with these steps poses additional challenges for large-scale production. Another challenge is the release of inhibitors during the pretreatment process which can result in a low PHA yield. The development of a low cost, co-culture strategy for the bioconversion of SCB into PHAs, can represent a pivotal step towards the large-scale production of bioplastics. This review highlights the advancements made in recent years on the microbial production of PHA using SCB as potential feedstock, with a proposed biological strategy and circular economy model.

Keywords: agricultural waste; bioplastics; circular economy; co-culture; lignocellulosic biomass; polyhydroxyalkanoate; sustainability

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1. Introduction

Due to their various mechanical properties, plastics are ubiquitously used in daily life and industry. The global production of plastics reached 390.7 million tonnes (Mt) in 2021, including fossil-based (350 Mt), recycled (32.5 Mt) and bio-based plastics (5.9 Mt), with an estimation to reach 760 Mt by 2050 [1]. In general, at the end of life, plastic waste is managed by landfilling and incineration [2,3]. It has been reported that around 80% of plastic waste is sent to landfilling, while 12% is incinerated [4]. However, both disposal methods lead to the release of toxic by-products, threatening ecosystems. Fossil-based plastics consist of 90.2% of the total yield of plastics [1]. This type of plastic is known for its low biodegradability and thus its complete degradation may take years to centuries [5]. Due to plastic's low biodegradability, together with poor waste management, plastic pollution has become one of the most significant environmental threats impacting both terrestrial and aquatic environments. It is estimated that around 30 million tonnes of plastic waste have leaked into oceans and seas, and a further 109 million tonnes have flowed into rivers, causing potential toxicological and physical risks to the aquatic ecosystem [6,7]. Therefore, as an alternative to fossil fuel-derived plastics, bioplastics would help to tackle the plastic pollution problem.

Recently, bioplastics have attracted attention as the world shifts towards sustainable and renewable resources. Compared to fossil-based plastics, bioplastics are characterised by their biodegradability and sustainability which make them a potential environmentally

friendly alternative to petroleum-derived plastics [8]. It has been reported that bioplastics can be completely biodegraded to biomass, carbon dioxide (CO_2) and water within 2 months under standard conditions [9], which would in the long term significantly reduce future plastic pollution and its severe impact on the environment.

Polyhydroxyalkanoates (PHAs) are a family of biodegradable polymers synthesised by a broad range of microorganisms, i.e., bacteria and archaea, as an energy storage compound in the form of lipid granules [10]. These biopolymers have similar mechanical characteristics to petroleum-derived plastics in terms of flexibility, elasticity, versality, etc., which make them one of the most investigated classes of bioplastics [11].

Despite the increasing market interest in PHAs and the significant number of studies, the production of PHAs is still limited to pilot scale. According to European bioplastics database [12], bioplastics production represented less than 1% of the total plastic production in 2022. One of the main restrictions for the large-scale production of PHAs is the high cost of production, which is approximately six times higher than the cost of petroleum-derived plastics [13]. The carbon source used as a feedstock is the main reason for the high production cost, accounting for around 50% of the total production cost [14,15]. Therefore, it is necessary to find cheap and efficient alternative substrates to increase the economic feasibility and sustainability of PHA production. Recently, researchers have started to explore the use of different low-cost substrates such as whey [16,17], glycerol [18,19], molasses [20,21], oils [22,23] and wastewater [24] for the biosynthesis of PHAs.

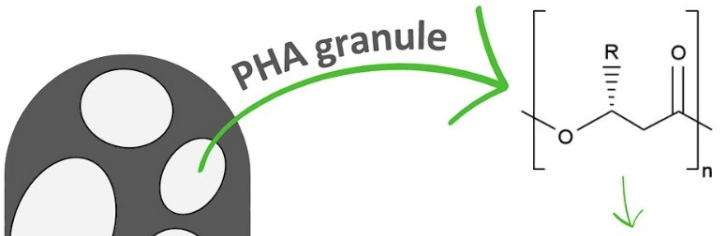
The use of renewable, cheap, and abundantly available feedstocks, such as agricultural waste, is also an option. Agricultural wastes are residues produced in the process of agricultural production and include crop residues, leaf litter, bagasse, sawdust, and peels [25]. This type of waste consists one of the largest categories of waste produced worldwide, with an estimated 998 Mt generated annually [26]. The lignocellulosic residues can be considered as promising feedstocks for PHA production due to their abundant availability, low cost, and lack of competition with human and food supply [27]. Cellulose and hemicellulose are the main compounds of lignocellulosic residues and their hydrolysis releases fermentable sugars [28]. These sugars can be turned into PHAs via biological processes by PHA-producing microorganisms. Several studies have investigated the use of agricultural waste such as food residues, bagasse, straws, corn cob and spent coffee grounds for PHA production [29–33].

One of the most abundant agricultural lignocellulosic wastes in tropical and subtropical regions is sugarcane bagasse (SCB). PHAs can be efficiently produced through integration into a sugarcane mill [34]. Besides being a cheap feedstock for PHA production, SCB can also be incinerated to generate the energy required for the production process. Hence, PHA production from SCB is an economically viable option due to the accessibility of a low-cost carbon source and energy. While several reviews discuss the use of different wastes to produce bioplastics, none have fully examined the use of SCB for the biosynthesis of PHA. This review highlights the recent advancements in research on the microbial production of PHA using SCB as potential feedstock. This includes a discussion of the pretreatment strategies, enzymatic hydrolysis, and accumulation of PHA by different microorganisms using this agricultural waste. In addition, the challenges associated with the use of SCB in PHA biosynthesis, which impacts its feasibility at a large scale, are discussed. To overcome these challenges, a biological strategy, co-culture, is suggested and discussed. Finally, an example of a circular economy model is proposed.

2. Structure and Composition of Polyhydroxyalkanoate

PHAs are biodegradable and biocompatible thermoplastics, soluble in chlorinated solvents, insoluble in water and resistant to hydrolytic attack and UV [35]. These biopolymers are polymerised polyoxoesters of polyesters of hydroxyalkanoates synthesised intracellularly by a wide range of microorganisms in the form of granules, with diameters ranging between 0.2 and 0.5 μm (Figure 1) [10,36,37]. The physical and chemical properties of PHAs, such as melting point, crystallinity, hydrophobicity, etc., differ significantly depending

on the composition of the monomers [38]. PHAs also have a wide range of mechanical characteristics which vary from hard to elastic thermoplastics according to the type of feedstock, microbial host and fermentation strategy [38–40].



n	R Group	PHA	Abbreviation
n=1	Hydrogen	Poly-(3-hydroxypropionate)	PHP
	Methyl	Poly-(3-hydroxybutyrate)	PHB
	Ethyl	Poly-(3-hydrovalerate)	PHV
	Propyl	Poly-(3-hydroxyhexanoate)	PHHx
	Pentyl	Poly-(3-hydroxyoctanoate)	PHO
	Nonyl	Poly-(3-hydroxydodecanoate)	PHDD
n=2	Hydrogen	Poly-(3-hydroxybutyrate)	P4HB
n=3	Hydrogen	Poly-(5-hydrovalerate)	P5HV

Figure 1. General structure of polyhydroxyalkanoates accumulated in bacteria in the form of granules. Polyhydroxyalkanoates are classified as short chain length (scl-PHAs), medium chain length (mcl-PHAs) and long chain length (lcl-PHAs). The table insert shows different PHA derivatives.

The classification of PHAs depends on the number of carbon atoms present in their hydroxyacid chain, consisting of three classes including short chain length (scl-PHAs) with 3–5 carbon atoms, medium chain length (mcl-PHAs) with 6–14 carbon atoms and long chain length (lcl-PHAs) with more than 14 carbon atoms in each monomer unit [10,41,42]. Due to differences in structure, the physical and mechanical properties of scl-PHAs differ from mcl-PHAs. For example, scl-PHAs have a significantly higher melting point than mcl-PHAs, which have a greater elasticity than scl-PHAs [43]. More than 150 monomers of PHAs have been reported to date with different structures including saturated, unsaturated, straight, branched and aromatic with poly(3-hydroxybutyrate) (PHB) being the most synthesised monomer [43]. Depending on the type of monomers and composition, PHAs can be classified as homopolyesters with only one monomer type or heteropolyesters with two or more monomer types [44].

3. Microbial Production of Polyhydroxyalkanoates and Different Pathways

PHAs are synthesised by different microorganisms, including bacteria and archaea such as *Bacillus*, *Pseudomonas*, *Acinetobacter*, *Legionella*, *Agrobacterium*, *Halobacteriaceae*, to sustain energy balance in the cell [45]. There are two groups of microbes involved in PHA production [46]. The first group includes growth-associated microorganisms, such as recombinant *Escherichia coli,* which accumulate PHAs during their exponential phase. The second group consists of non-growth-associated microbes, such as *Pseudomonas oleovorans,* which synthesise PHAs under stress due to an excess in carbon, limitation of oxygen, nitrogen or phosphorus, and extreme conditions. Classical strain improvement and metabolic engineering have also been broadly applied to generate PHA-producing engineered microorganisms in order to improve PHA production [13].

Among the different PHA-producing bacteria, *Burkholderia cepacia* and *Cupriavidus necator*, previously known as *Ralstonia eutropha* and *Wautersia eutropha* [47], are known for their ability to accumulate up to 75% and 90% (% of CDM) of their cellular mass as PHA and for using different substrates as carbon sources [48,49]. Several *Bacillus* species such as *Priestia megaterium* (previously known as *B. megaterium* [50]) have also been used to produce PHA due to their high growth rate, absence of lipopolysaccharide cell membrane

which facilitates the extraction process, and the ability to produce enzymes that hydrolyse complex substrates for simpler carbon sources [51].

The microbial synthesis of PHA involves three different pathways, which depend on the general metabolism of the microbial host (Figure 2). Scl-PHAs are synthesised by bacteria such as *Cupriavidus necator* through the glycolysis of sugars via pathway I. This pathway involves three key enzymes including 3-ketothiolase, acetoacetyl-CoA reductase and PHA synthase encoded by three genes, *phaA*, *phaB* and *phaC*, grouped together on the *phaCAB* operon, respectively. Following the glycolysis of glucose, 3-ketothiolase converts two molecules of acetyl-CoA into one molecule of acetoacetyl-CoA. Acetoacetyl-CoA is then converted into 3-hydroxybutyryl-CoA by acetoacetyl-CoA reductase. Finally, an ester-bond is formed between 3-hydroxybutyryl-CoA molecules to produce a polymer such as PHB [52]. Mcl-PHAs are synthesised via pathway II and III, such as in *Pseudomonas* sp. through different types of precursors and enzymes. Pathway II involves the production of PHAs from the breakdown of lipids and fatty acids by the β-oxidation cycle [53]. In this pathway, different hydroxyacid monomers are synthesised by the activity of acyl-CoA oxidase, (R)-specific enoyl-CoA hydratase, and 3-ketoacyl-CoA reductase. Polyhydroxyalkanoate synthase then joins the monomer molecules to produce PHA polymers [46,54]. *Pseudomonas aeruginosa* is an example of bacteria that use pathway II to produce mcl-PHAs [55]. Pathway III emphasises the production of PHAs from simple carbon sources such as methanol and carbon dioxide (CO_2) [56]. The *phaG* gene encodes for an acyl-ACP-CoA transacylase enzyme which is responsible for the transformation of intermediates generated in the fatty acid biosynthesis pathway to COA form [57].

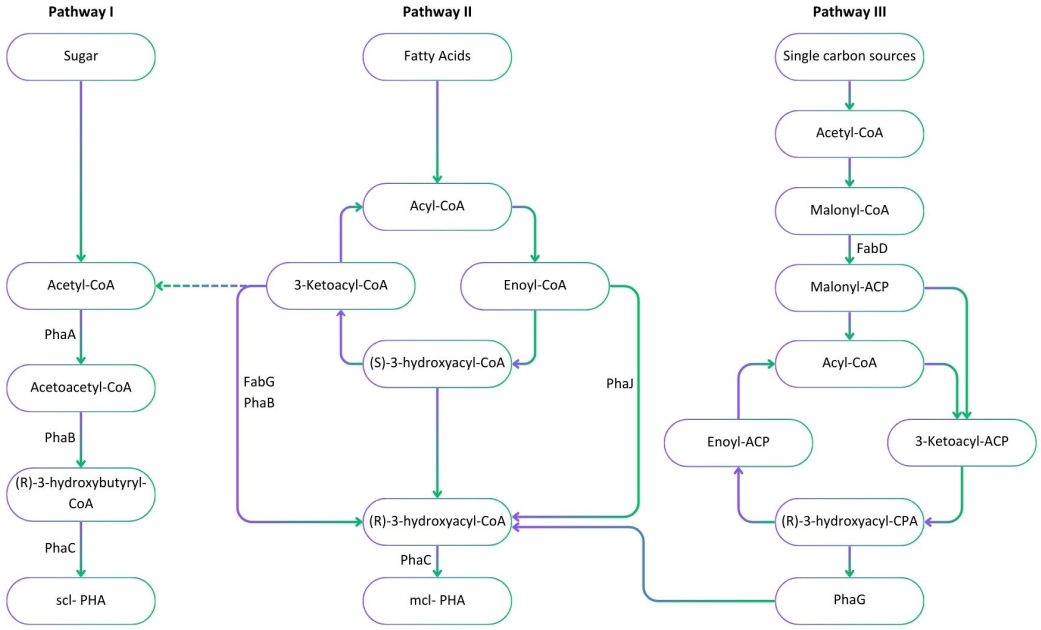


Figure 2. Metabolic pathways including precursors and enzymes involved in the microbial synthesis of PHAs from sugars through glycolysis (pathway I), fatty acids through β-oxidation (pathway II) and simple carbon sources through the de novo synthesis of fatty acids (pathway III). The major enzymes involved in the production process are PhaA: 3-ketothiolase; PhaB: acetoacetyl-CoA reductase; PhaC: PHA synthase; PhaG: (R)-3-hydroxyacyl-ACP-CoA transferase; PhaJ: (R)-specific enoyl-CoA hydratase; FabD: Malonyl CoA-acyl carrier protein (ACP) transacylase; and FabG: 3-ketoacyl-ACP reductase.

4. Sugarcane Bagasse: An Abundant Substrate for Polyhydroxyalkanoate Production

Sugarcane, *Saccharum officinarum*, is a major crop in tropical and subtropical regions, with its juice being the main feedstock to produce sugars in sugar mills. With around 1870 Mt produced annually, sugarcane contributes more than 70% of the global sugar demand and is one of the largest feedstocks for biofuels production globally [58].

Numerous waste products are generated during the processing steps of sugarcane including sugarcane straws as harvest residues, bagasse after sugar extraction, molasses, etc. Compared to the world's other major crops such as wheat, rice and corn, sugarcane produces the highest crop residues yield per unit area and the highest lignocellulosic content, some three to four times higher than other major crops [59]. Sugarcane bagasse (SCB) is obtained after a series of milling steps to extract sugars from sugarcane. Theoretically, for every tonne of sugarcane, 0.3 tonnes of bagasse is generated. This residual waste is considered one of the largest agricultural wastes globally, with an annual production of 513 Mt [60]. A significant fraction of SCB is usually disposed of in an uncontrolled way as waste piles in open lands, resulting in serious environmental problems including the release of unpleasant odours arising from the decomposition of waste, greenhouse gas emissions, land contamination and occasionally self-igniting fires [61]. When not landfilled or disposed of, SCB is inefficiently incinerated for the generation of electricity in sugar mills, which results in a loss of around 65% of its energy content, in addition to the emission of a significant amount of carbon dioxide [62]. In contrast, bagasse can be converted into valuable products due to its high polysaccharide content, which consists of around 60–80% of its wet mass [63]. For example, monosaccharides, resulting from the hydrolysis of polysaccharides in bagasse, can be fermented by microbes into biofuels, biopolymers such as PHAs [64]. Moreover, due to its fibrous nature, SCB can potentially be used in the production of sound adsorbers and thermal insulation [65]. The use of SCB to produce PHAs offers several advantages as it is considered a sustainable source for PHA production that does not compete with food production, which addresses the concern associated with the use of food crops to produce biopolymers [41]. Moreover, the use of such agricultural residues represents a form of waste valorisation, by converting SCB into a valuable bioplastic, thus reducing its negative impact on the environment. In addition, using SCB as a feedstock reduces the dependency on fossil fuels used to produce conventional plastics which consume around 20% of global oil and gas [66]. Overall, the production of PHA using SCB as a carbon source aligns with the concepts of circular economy, sustainability and a transition towards greener products.

5. The Structure and Composition of Sugarcane Bagasse

The structure and composition of SCB have been extensively studied [64,67]. Bagasse is a fibrous waste consisting of about 40–45% fibres, 45–50% water and 2–5% dissolved sugars [68]. The fibres are mostly composed of cellulose (40–50%), hemicellulose (25–35%) and lignin (20–30%) [69]. Cellulose and hemicellulose are embedded in the lignin matrix which helps to improve the rigidity of the bagasse [63]. Cellulose consists of -D-glucose bonded by β-1,4-glycosidic bonds. Due to its high molecular weight and crystallinity, cellulose is not digested by humans and does not dissolve in water [70]. Hemicellulose is an amorphous polysaccharide and is composed mainly of xylose, with other sugars including galactose, mannose, arabinose and rhamnose [69]. Both cellulose and hemicellulose are valuable compounds in bagasse as they represent sustainable sources of fermentable sugars after hydrolysis. However, lignin is a phenolic macromolecule that is resistant to enzymatic degradation [71]. Therefore, the lignin percentage and distribution in SCB are considered major parameters in determining the resistance of bagasse to hydrolysis and thus sugars release [72].

6. The Production Process of Polyhydroxyalkanoates from Sugarcane Bagasse

Transforming complex polysaccharides into fermentable sugars is one of the major challenges in the use of SCB as a feedstock to produce PHAs and requires two essential steps: pretreatment and hydrolysis. After hydrolysis, monomeric sugars are fermented by PHA-accumulating bacteria. The pretreatment of SCB is required for the removal of lignin, decrystallisation of glucose and partial depolymerisation of hemicellulose to increase the porosity of bagasse and facilitate the access of enzymes during the hydrolysis step [73]. Consequently, both polysaccharides, cellulose and hemicellulose, can be hydrolysed to

monosaccharides, making SCB a potential raw material for the biosynthesis of PHA. Generally, a biorefinery aims to sustainably convert biomass, in an optimal matter, to produce high-value products. To accomplish this, an SCB-based biorefinery should combine several biotransformation processes to utilise each lignocellulosic component of bagasse, resulting in an adequate yield and valorisation of cellulose, hemicellulose, and lignin. It has been reported that with appropriate pretreatment and an efficient enzymatic hydrolysis, 90% of the total reducing sugar yield from a lignocellulosic biomass can be utilised [74]. A general scheme presenting the production of PHA from SCB is shown in Figure 3.

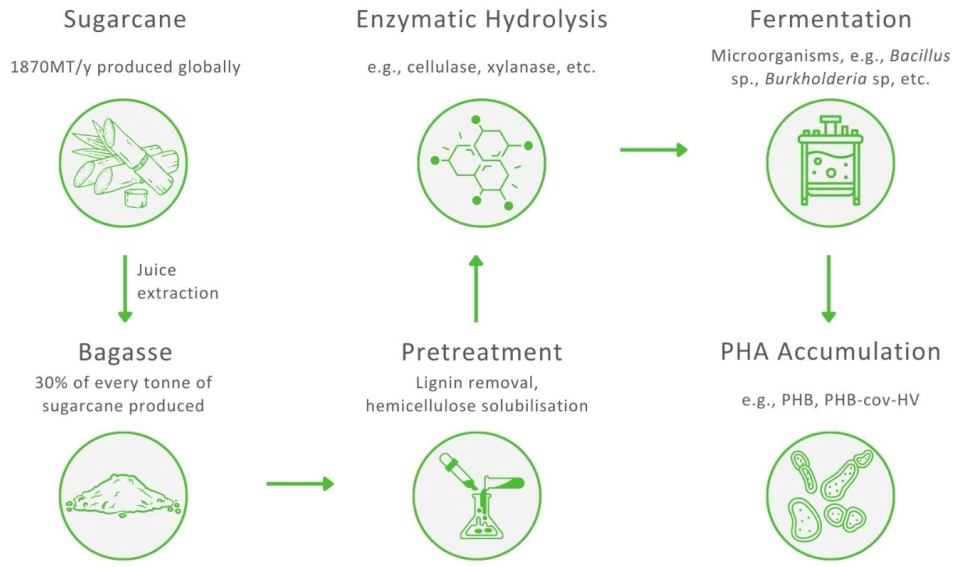


Figure 3. The process of the production of polyhydroxyalkanoates from sugarcane bagasse.

6.1. Pretreatment of Sugarcane Bagasse

The pretreatment of SCB allows the removal of lignin and the breakdown of the lignocellulosic structure [75]. Pretreatment strategies have been applied to lignocellulosic materials, including SCB, to reduce their recalcitrance and improve the release of fermentable sugars following enzymatic degradation. The pretreatment of lignocellulose may be conducted using chemical, physical or biological processes. Pretreatment is considered effective if it accomplishes the following: (1) enhances the release of fermentable sugars; (2) preserves the structure of carbohydrates; (3) limits the formation of by-products, i.e., inhibitors; and (4) is economically feasible [76]. Many pretreatment methods have been performed on SCB with the most common methods being dilute acid hydrolysis, alkaline pretreatment, steam explosion, organosolv pretreatment, liquid hot water and biological pretreatment. Table 1 shows some examples of different pretreatments for SCB and their outcomes.

Table 1. Advantages and disadvantages of pretreatments with examples of sugarcane bagasse pretreatments from the literature.

Pretreatment	Experimental Conditions	Experimental Outcomes	Advantages	Disadvantages	Reference
Dilute acid hydrolysis	1% H_2SO_4, 120 °C for 40 min.	Removal of 55% of holocellulose, 32.9% of lignin and 83% sugar yield.	Efficient removal of lignin. High solubility of hemicellulose. Efficient sugar recovery. Low-cost application.	Specialised equipment required. Corrosive process. Formation of inhibitors.	[77]
	1% H_2SO_4, 1% CH_3COOH, 190 °C for 10 min.	Removal of 90.9% of hemicellulose and 76% sugar yield.			[78]

Table 1. *Cont.*

Pretreatment	Experimental Conditions	Experimental Outcomes	Advantages	Disadvantages	Reference
Alkaline pretreatment	3% NaOH, 50 °C for 240 min.	Removal of 78.6% of lignin and 39% sugar yield.	Efficient removal of lignin. Decrease in cellulose crystallinity. Low formation of inhibitors.	Partial solubilisation of hemicellulose. Enzymes needed for sugar recovery. High water usage for washing.	[79]
	0.5 M Na_2CO_3, 140 °C for 80 min.	Removal of 83% of lignin, 18.6% cellulose yield and 21.4% xylose yield.			[80]
Steam explosion	0.01 mol L^{-1} $C_6H_8O_7$, 180 °C, 863 kPa for 5 min.	Removal of 41% of hemicellulose and 14.3% of lignin.	Eco-friendly process. No specialised equipment required.	High temperatures required. Formation of inhibitors.	[81]
Organosolv pretreatment	0.5% H_2SO_4 and 95% glycerol, 121 °C for 10 min.	Hydrolysis of 42% of cellulose.	Major removal of lignin and hemicellulose.	Use of volatile solvents. High cost due to solvent use.	[82]
Liquid hot water	Water with C_2H_6O, 160 °C for 60 min.	Removal of 16.9% of lignin.	Short reaction time. No chemicals required. Improved saccharification efficiency.	High temperature required. Formation of inhibitors.	[83]
Biological pretreatment	500 mg *Ceriporiopsis subvermispora* per kg of SCB, 27 °C for 60 days.	Removal of 47% of xylan and 48% of lignin.	Eco-friendly and sustainable process. No required chemicals. Low energy consumption.	Long reaction time. Low hydrolysis efficiency.	[84]

$C_6H_8O_7$: Citric acid; C_2H_6O: Ethanol.

Pre-hydrolysis with dilute acid has been demonstrated to be an effective method for lignocellulosic biomass such as SCB [85]. Sulfuric acid is the most widely used acid to treat bagasse; however, other acids such as hydrochloric, phosphoric, and nitric acid can also be employed [86]. Many studies on dilute acid pretreatment using sulfuric acid have shown the effectiveness of this acid on sugarcane bagasse. For example, Zhao et al. [87] reported that pretreating SCB with 2% sulfuric acid for 2 h at 121 °C allowed the solubilisation of 85% of the hemicellulose and the elimination of 16% of the lignin content. Due to its low cost and convenient application, dilute acid pretreatment is the most used pretreatment for bagasse to produce PHA [88–93]. However, the disadvantage of this method is the formation of different types of inhibitors, such as phenolic compounds from lignin degradation, and furfural, hydroxymethylfurfural (HMF) and acetic acid from hemicellulose and cellulose degradation [94]. These inhibitors have negative effects on the microbial fermentation [95].

Alkaline pretreatment is another chemical pretreatment strategy used for SCB. This pretreatment is considered a cost-effective process with less inhibitors produced [96]. Several bases can also be used, such as sodium hydroxide (NaOH) [97,98], potassium hydroxide (KOH) [99], calcium hydroxide ($Ca(OH)_2$) [100], ammonia (NH_3) [101] and a combination of NaOH and hydrogen peroxide (H_2O_2) [102]. Yu, Tan, Sun, Nishimura, Takei, Tang and Kida [98] reported that treating SCB with NaOH (1%) for 10 min at 120 °C removed 67.5% of lignin. Similarly, Zhang et al. [103] reported that using NaOH with H_2O_2 in the pretreatment of SCB resulted in a significant breakdown of lignin, hence improving the enzymatic digestibility of the bagasse. The main disadvantage of this pretreatment is that the use of sugars released from hemicellulose is more difficult than in the case of dilute acid pretreatment. This is because most of the hemicellulose content remains in the

residual bagasse even after alkaline pretreatment, hence the need to add hemicellulolytic enzymes such as xylanase in the following hydrolysis step [104].

It has also been demonstrated that organosolv pretreatment is effective to pretreat bagasse in many studies. Schmatz and Brienzo [105] were able to remove 45.3% of lignin and 72.5% of hemicellulose from SCB after pretreatment with 50% ethanol at 121 °C. Similarly, Zhang et al. [106] reported the effective removal of 75.5% lignin after pretreating bagasse with 60% ethanol and 5% NaOH at 180 °C. This pretreatment employs an organic solvent with high concentrations ranging from 30 to 70% at temperatures of 100–200 °C in the presence or absence of a catalyst [107]. One drawback of organosolv pretreatment is the high cost compared to other leading pretreatments [108].

As a physical pretreatment, steam explosion is an eco-friendly technology which allows the fractionation and recovery of the three main components of SCB in high yield [109]. For instance, Silveira et al. [110] pretreated SCB by steam explosion using a 65 L reactor. The pretreatment resulted in 85% hemicellulose solubilisation, proving the efficiency of this technique. Pitarelo et al. [111] also used steam explosion in the presence of H_3PO_4 with a concentration of 19 mg g^{-1} to pretreat SCB. Pretreatment at 180 °C for 5 min was reported to be optimal, with a total sugar yield of 75% after hydrolysis. In addition to steam explosion, liquid hot water is a green technology that can be considered a potential pretreatment method to pretreat SCB. Zhang, You, Lei, Li and Jiang [83] reported that the acetyl-assisted hot water pretreatment of SCB with water for 70 min at 160 °C resulted in 9.8 g L^{-1} of xylose. Moreover, it has been reported that autohydrolysis can alter the surface morphology of SCB and improve the saccharification efficiency [112].

Biological pretreatment is an environmentally friendly method based on employing suitable cellulolytic and hemicellulolytic enzymes or microorganisms to degrade lignocellulosic biomass [113]. This pretreatment requires less energy and generates fewer inhibitors compared to chemical and physical pretreatments [114]. However, the long biodegradation period limits the further development and use of this pretreatment method by industries [84]. Microorganisms, including fungi and bacteria, isolated from different environments such as soil and lignocellulosic waste can be used for biologically pretreating SCB. To date, few studies evaluating the biological pretreatment of SCB have been reported [84]. However, some studies have shown that the use of fungi enhances the digestibility of polysaccharides, while very few microorganisms are able to fully decompose lignin in SCB [115–117]. Microbial consortium pretreatment has been used on lignocellulosic biomass to increase biogas production [118,119]. However, its use to pretreat SCB to increase PHA production has not been fully investigated. This pretreatment method does not require the sterilisation of biomass in the case of using pure culture [85]. Generally, the use of biological pretreatments to treat lignocellulosic biomass is not as effective as chemical pretreatments due to its long degradation time and high selectivity of microbes. Further studies are needed to overcome these issues and enable the use of this green pretreatment efficiently.

6.2. Hydrolysis of Polysaccharides in Treated Sugarcane Bagasse

Following pretreatment, SCB undergoes hydrolysis to transform cellulose and hemicellulose into monomeric sugars to produce PHA. This step facilitates the availability and solubility of the carbon source to be used by bacteria. Generally, acid treatment and enzymatic hydrolysis are the major methods employed. However, enzymatic hydrolysis is favoured over acid hydrolysis as it is environmentally friendly, releases less inhibitors, does not require corrosion resistant equipment, and most importantly, leads to an almost complete hydrolysis of cellulose content in SCB, resulting in a high PHA yield [120,121]. Cellulase is responsible for the hydrolysis of cellulose by cleaving the β-(1–4)-D-glucose. There are three types of cellulases involved in hydrolysis; endoglucanases, exocellobiohydrolases and β-glucosidase [122]. These cellulases break down the cellulose into monosaccharides, mainly glucose molecules. In contrast, many enzymes are required for the hydrolysis of hemicellulose, such as xylanases, arabinofuranosidase and glucuronidase [121]. Due to its

branched structure, hemicellulose is readily hydrolysed to mainly xylose, galactose, and arabinose [123]. Several bacterial and fungal microorganisms can hydrolyse polysaccharides from lignocellulosic biomass into fermentable sugars. Bacteria belonging to the genera *Streptomyces*, *Bacillus* and *Clostridium* have been reported as cellulolytic bacteria [124]. In addition, fungi such as *Trichoderma*, *Penicillium* and *Aspergillus* exhibit a wide range of cellulase enzymes which play a key role in the hydrolysis of lignocellulosic biomass [125]. Although research on hydrolysis by microorganisms has been conducted and some progress has been reported, the use of bacteria and fungi is rarely carried out due to the long incubation time required to achieve hydrolysis [126]. Usually, commercial enzymes are applied to achieve an efficient hydrolysis rate.

7. The Status of the Production of Polyhydroxyalkanoates from Bagasse

Studies on PHA production using SCB hydrolysates have focused on optimising both culture conditions and experimental parameters to achieve high yields. Batch culture approaches has been the most applied system reported. While a wide range of biopolymers are produced by bacteria, PHB is the main polymer produced from SCB (Table 2). Several factors affect the yield of PHA from SCB including the microorganism used, the mode of culture (pure, co-, or mixed culture), and experimental parameters such as incubation time, pH, inoculum density, temperature, carbon to nitrogen ratio (C/N) and oxygen concentration [127]. The optimisation of experimental parameters depends on the microorganism and the mode of culture used to produce PHA. Currently only a few microorganisms have been investigated for their potential to produce PHA from SCB (Table 2). *Bacillus* spp. was used to produce PHB from pre-treated SCB and achieved a polymer content of 56% [30]. In another study, *Burkholderia* sp. was able to utilise SCB hydrolysate and produced PHB with 49% polymer content [128]. However, a PHB content of 61.5% was achieved when *Lysinibacillus* sp. utilised SCB hydrolysate with 2% corn steep liquor [129]. Madhumathi et al. [130] reported that, compared to other agrowastes such as molasses, rice bran, wheat bran and whey waste, SCB showed the maximum PHA yield with a concentration of 6.4 g L^{-1} and an accumulation of about 70% by *Bacillus safensis*. This can be explained by the high cellulose content in SCB that was converted into glucose, readily utilised by *Bacillus safensis*.

The efficiency of enzymatic hydrolysis depends on several parameters including the structure of pretreated SCB, enzyme loading and the hydrolysis period [122]. According to several economic analyses, the steps of releasing sugars from lignocellulosic biomass, including pretreatment and hydrolysis (the production and purification of enzymes), contributes to around 45% of the total cost, with the cost of cellulase enzyme being between \$0.2 to \$0.4 per litre of the final product [120]. The high cost associated with pretreatment and the use of enzymes currently hinders the use of SCB at a large scale for PHA production. Therefore, reducing these significant costs is a key concern for making SCB utilisation a commercially viable process. Catabolite repression is also considered one of the factors responsible for the low yield of PHA, where the presence of one carbon source controls the use of others in the culture medium; that is, bacteria selectively assimilate only one carbon source among many other sources present in the medium, resulting in low productivity [131]. As previously stated, glucose and xylose are the main sugars released following the hydrolysis of SCB. As bacteria generally prefer the C6 sugar, glucose, this causes an accumulation of the C5 sugar, xylose, and other sugars, which results in an inefficient bioconversion of SCB into PHA. An important exception has been reported recently by Kourilova et al. [132] who demonstrated that the thermophilic strain of *Schlegelella thermodepolymerans* (now *Caldimonas thermodepolymerans* [133]) prefers xylose over other sugars including glucose, arabinose fructose, galactose, mannose, and lactose and accumulates a considerable amount of PHA using xylose-rich resources. Moreover, the release of inhibitors during the pretreatment of SCB can significantly affect the growth of PHA-producing bacteria [134]. Therefore, further research is required in terms of the optimisation and improvement of PHA synthesis from SCB. Additionally, there is a need to

investigate more microbial strains for their ability to use more than one carbon source from the SCB hydrolysate mixture.

Table 2. Studies in the literature using sugarcane bagasse (SCB) hydrolysates as feedstock to produce polyhydroxyalkanoates (PHA).

Microorganism	Mode of Culture	Type of PHA	Dry Cell Weight (g L^{-1})	PHA Accumulation (% CDW)	PHA Titre (g L^{-1})	Reference
Lysinibacillus sp. RGS	Batch	PHB	8.7	61.5	5.3	[129]
Klebsiella pneumoniae G1	Batch	PHB	22.5	40	9	[135]
Bacillus safensis EBT1	Batch	PHB	9.2	69.5	6.4	[130]
Burkholderia sp. *F24*	Batch	PHB PHB-co-HV	9.8	49	4.72	[128]
Halogeometricum borinquense strain E3	Batch	PHB-co-HV	4.2	45.7	1.9	[136]
Burkholderia sacchari IPT101	Batch	PHB	4.4	62	2.7	[137]
Burkholderia cepacia IPT048	Batch	PHB	4.4	53	2.3	[137]
Bacillus sp.	Batch	PHB	9	55.6	5	[30]
Ralstonia eutropha	Batch	PHB	6	65	3.9	[138]
Burkholderia glumae MA13	Batch	PHB	0.61	14.9	9	[139]
Bacillus thuringiensis IAM 12077	Batch	PHB	10.6	39.6	4.2	[140]
Bacillus megaterium PNCM 1890	Batch	PHB	4.9	40.8	2	[141]
Bacillus sp.	Batch	PHB	9	55.6	5	[30]

PHB: poly(3-hydroxybutyrate); PHB-co-HV: poly(3-hydroxybutyrate-*co*-3-hydroxyvalerate).

8. Co-Culture: A Strategy to Address Polyhydroxyalkanoate Production Challenges

The microbial production of bioplastics using SCB supports the concept of a circular economy. Nevertheless, this review has highlighted some challenges which hinder the feasibility of producing bioplastics from this feedstock at an industrial scale. To address these challenges, co-culture can be applied to enhance PHA production. Co-cultures are biological systems where two or more different microorganisms naturally or artificially grow together within a medium [142]. This biological system has the potential to mitigate some challenges associated with the production of PHA from SCB, as it leads to the tolerance of bacteria against inhibitors released during pretreatment, the promotion of enzymatic hydrolysis and the bioconversion of several sugars into PHA within the culture medium.

Recently, there has been increasing interest in the use of synthetic co-cultures for PHA production [49,143]. However, the use of co-cultures is currently reliant on the use of expensive soluble sugars extracted from different plant biomass [144–146], while the use of lignocellulosic feedstocks including SCB remains a significant challenge. Currently there are only few studies that have used co-cultures to produce PHA from lignocellulosic biomass. As an example, Saratale, Cho, Kadam, Ghodake, Kumar, Bharagava, Varjani, Nair, Kim, Shin and Saratale [134] developed a microbial co-culture system of *Lysinibacillus* sp. RGS and *Ralstonia eutropha* ATCC 17699 to enhance PHA production using acid pretreated SCB. The co-culture strategy showed higher assimilation of SCB hydrolysates and stimulated bacterial growth compared to individual strains. This study demonstrated that the use of co-culture could result in an effective utilisation of SCB, due to a synergetic effect of the

bacterial strains used in the experiment. Another study investigated the use of two bacterial strains: the cellulolytic bacteria *Streptomyces* sp. SirexAA-E and the PHA-producing bacteria *Priestia megaterium* NBRC 15308, where neither strain could produce PHA from *Miscanthus* grass alone. However, co-culturing both strains allowed the production of PHA without any addition of hydrolysis enzymes [147]. Co-culture can also be employed to overcome the catabolite repression of some sugars. In a study conducted by Lee et al. [148], to avoid the inhibiting effect of glucose, *Bacillus* sp. SM01, a xylose-utilising bacterium was co-cultured with *Cupriavidus necator* NCIMB 11599, which is known for its inability to assimilate xylose. The study showed an increase in PHA production of 40% compared to monoculture.

Compared to other microbial systems, microbial co-culture is more robust than a monoculture system, while it is less complex than mixed culture systems. Therefore, the co-culture approach is a potential alternative for the efficient bioconversion of lignocellulosic feedstocks into valuable biopolymers [49]. Studies on synthetic co-cultures have primarily focused on the use of a broader range of simple substrates, the neutralisation of toxic by-products and the synthesis of mcl-PHAs [49,144,149–151]. However, research on the use of synthetic co-culture systems to produce PHA from complex substrates such as SCB is still at an early stage and needs more investigation in terms of exploring microbial interactions and bioprocess optimisation. In addition to investigating microbial interactions, exploration of the robustness of the co-culture systems and the effect of prolonged co-evolution during their application in the PHA production process is needed. Future studies must address these topics to have better understanding of the applicability of co-culture systems to produce PHA from lignocellulosic biomass such as SCB.

9. Circular Economy Model for Polyhydroxyalkanoate Production

Sugarcane is produced in tropical and subtropical areas in Australia with 95% grown in Queensland and about 5% in northern New South Wales [152]. Based on data provided by the Australian Sugar Milling Council, 30,090 kT of sugarcane was produced and crushed in 2021 (Figure 4) [153]. The milling and processing of sugarcane generated around 10,000 kT of bagasse [154]. Currently, sugarcane bagasse is used as a carbon-neutral fuel source to generate electricity [155]. The use of bagasse as a fuel source is desirable as it can generate more than one million MWh per year, of which 56% is used to power operations and 44% is exported to the grid, capable of powering up to 135,000 households (Figure 4) [156]. However, not all bagasse generated can be used as a fuel source; this is due to the high capital cost involved in establishing co-generation facilities. The current combined capacity of the 28 power stations utilising bagasse as a fuel source is 539 megawatts, with an estimated capital cost of around $1.5 billion [157].

It was reported by the National Waste Report that 10,300 kT of bagasse, in the form of available bagasse, was produced in Australia in 2021 [154,157]. While the fate of bagasse was not recorded, bagasse is generally transported off-site and disposed of in landfills, resulting in greenhouse gas (GHG) emissions [155,158]. This can incur high operational expenses as the estimated cost of landfills in Australia is between $42 to $101 per tonne of waste [159]. In addition, the disposal of bagasse into landfills will generate around 2.1 tonnes of CO_2-equivalent per tonne of waste [160]. In this current linear economy model, valuable resources arising from bagasse are lost and their disposal into landfills is not environmentally friendly (Figure 4).

The diversion of this valuable resource away from landfills and into PHA production can create a closed-loop, circular economy model for bagasse in Australia and tropical and subtropical regions of the world. Bagasse can undergo biological processes to produce PHAs, which can be turned into environmentally friendly bioplastics. The desirable features of PHAs, such as mechanical properties, biocompatibility, biodegradability and non-toxicity, make them suitable for diverse applications across various sectors including but not limited to industrial, environmental, and biomedical sectors. The application of PHAs in industries involves their use for packaging. For example, a copolymer (poly(3-hydroxybutyrate-co-3-hydroxyvalerate)), marketed as BIOPOL® was produced by Imperial

Chemical Industry Biological (ICI), London, UK, and used for the packaging of shampoo bottles and razors as well as disposable cups [161]. Another PHA, poly(3-hydroxybutyrate-co-3-hydroxyhexanoate)(PHBH), is industrially produced under the name of Nodax™ by Danimer Scientific, Bainbridge, GA, USA, and is applied in packaging carpet and compostable bags [38]. Due to its high filler loading ability, PHA can also be used with various natural fibre materials to develop biopolymer composites. For example, studies reported the use of PHB or PHBV with the reinforcement of SCB to produce PHA-based composites [162,163]. The biomedical application of PHA includes its use as a drug carrier, for implants, in tissue engineering, etc. [164]. In terms of environmental application, PHAs can be used as antimicrobial agents to control the outbreak of certain diseases. It has been reported that the use of PHB in aquacultures controls *Vibrio* infection in shrimp due to its antiadhesive property [165].

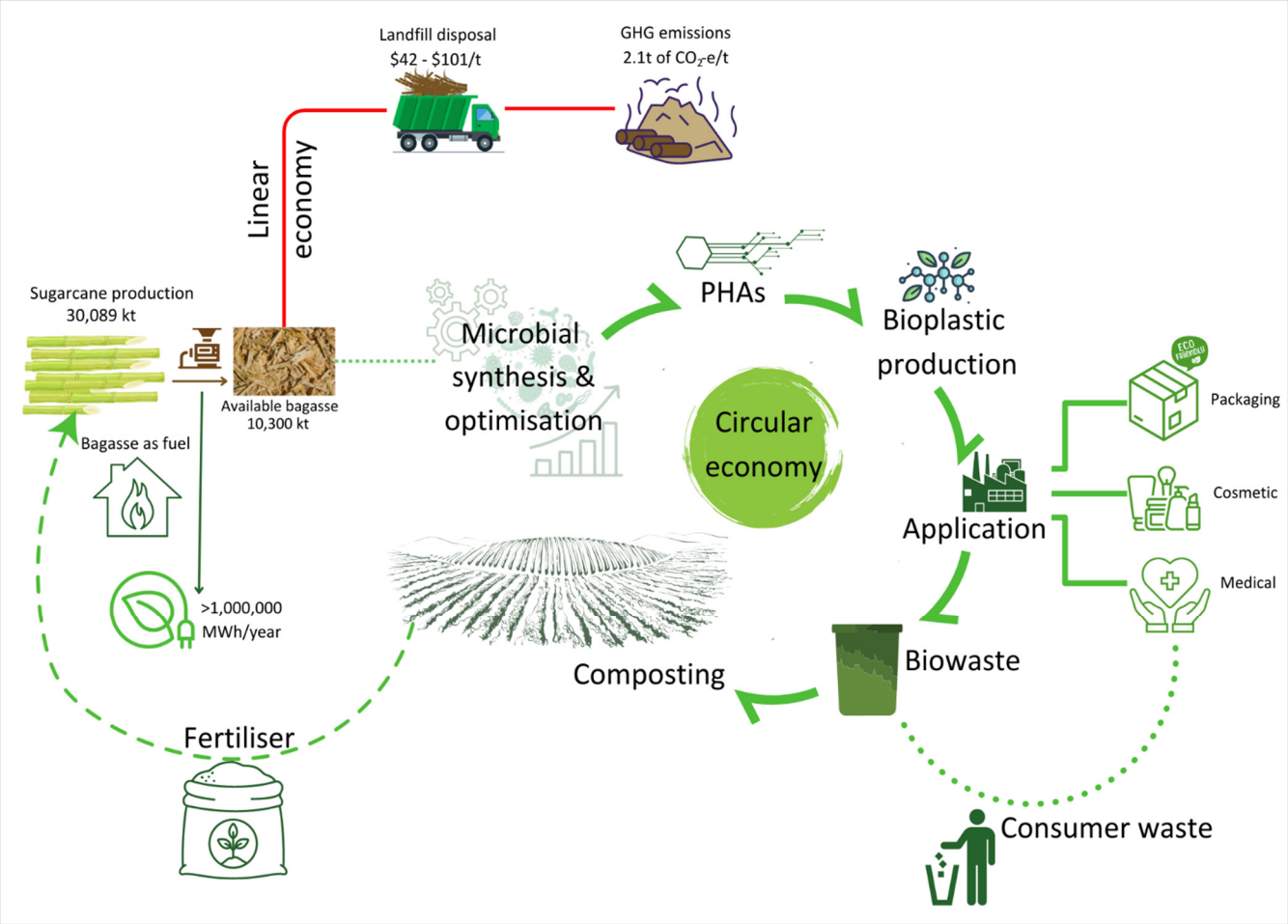


Figure 4. Comparison of linear economy and circular economy models arising from bagasse generation in Australia. Available bagasse refers to the proportion of bagasse that is not required for fuelling.

The biowaste arising from bioplastic applications, as well as from the consumption of bioplastic-derived products, can be composted. Compostable biopolymers are being developed and demonstrate a high degradation rate [166]. In the last ten years, researchers have explored the role of composting in the biodegradation of bioplastics [167–169]. This fertiliser can then be reapplied to sugarcane plantations, closing the waste loop of bagasse.

10. Conclusions

Plastic pollution has increased significantly in recent decades, posing health and environmental risks. Biodegradable plastics are a sustainable alternative to petroleum-derived plastics. One of these bioplastics is PHA, a biopolymer produced by microbes which shows promising chemical and physical properties, biocompatibility, and biodegradability. Despite the increasing market interest in PHAs, their production is not practical due to high production costs. A lack of a suitable carbon source is one of the major constraints for large-scale production. Therefore, finding a cheap carbon source to be used as a feedstock is a potential solution. While the concept of using agricultural waste to produce PHA is not new, innovative and new strategies are needed to reduce the cost associated with the production of PHA and improve the feasibility of producing these biopolymers at large scale. Currently, the selection of an efficient pretreatment of SCB with a high sugar recovery level and less inhibitors is considered a key factor to maximise the PHA yield. Moreover, the selection of the most suitable strains and culture strategies as well as the optimisation of the experimental conditions are crucial to achieve scale-up of PHA production. The development of an eco-friendly strategy employing the co-culture of PHA-producing microorganisms, which simplifies the steps in the conversion of SCB into bioplastics, and reduces the cost of production, would be a significant breakthrough for the PHA industry.

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