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Bioenergy, Biofuels and Biochemicals – Review

Purple non-sulfur bacteria for biotechnological applications

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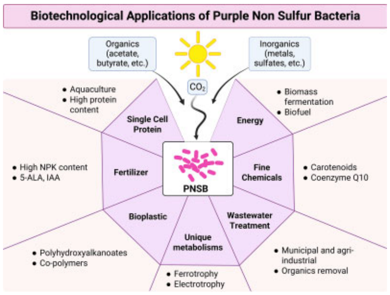
Abstract: In this review, we focus on how purple non-sulfur bacteria can be leveraged for sustainable bioproduction to support the circular economy. We discuss the state of the field with respect to the use of purple bacteria for energy production, their role in wastewater treatment, as a fertilizer, and as a chassis for bioplastic production. We explore their ability to serve as single-cell protein and production platforms for fine chemicals from waste materials. We also introduce more Avant-Garde technologies that leverage the unique metabolisms of purple bacteria, including microbial electrosynthesis and co-culture. These technologies will be pivotal in our efforts to mitigate climate change and circularize the economy in the next two decades.

One-sentence summary: Purple non-sulfur bacteria are utilized for a range of biotechnological applications, including the production of bio-energy, single cell protein, fertilizer, bioplastics, fine chemicals, in wastewater treatment and in novel applications like co-cultures and microbial electrosynthesis.

Keywords: Purple bacteria, Sustainability, Biotechnology, Waste, Bioproduction, Circular economy

Graphical abstract



Introduction

In 2022, the ever-increasing global population surpassed eight billion, continuing to exert a heavy burden on the environment and economy (Ritchie et al., 2022). Under a business-as-usual situation, waste production is projected to increase by 70% to 3.40 billion tons by 2050. This waste includes non-recyclable products such as synthetic plastics, as well as food and green waste, metals, paper, glass and more [not accounting for greenhouse gas (GHG)-producing energy and commercial processes] (Kaza et al., 2018). By 2050, total food demand is expected to increase by more than 30%, putting up to 8% of the global population at risk of hunger (AbdelRahman, 2023; Van Dijk et al., 2021). To mitigate the negative effects of our current production processes and answer the demand for basic resources, the world must move toward a sustainable circular economy (CE). The CE focuses on reusing, reducing, and recycling with renewable inputs, rather than dead-end resources such as petroleum (Kirchherr et al., 2023). The goal is to promote both economic development and environmental sustainability, a feat that many countries display great enthusiasm for but struggle to implement (Vogiantzi & Tserpes, 2023). As such, it is critical to develop methods that will promote the effectiveness of the CE, namely approaches that focus on incorporating lost or "waste" components, such as end-of-life products, back into value-added products or processes, like energy generation. A major player in building this economy will be microorganisms that fix carbon and remove GHGs, produce valuable compounds for the energy, food, and pharmaceutical industries, and remediate toxic wastes (Jain et al., 2022). One group of microorganisms that can perform all these functions, making them an attractive target for contributing to the CE, are the purple non-sulfur bacteria (PNSB).

PNSB possess some of the most versatile metabolisms in the microbial world, and as mixotrophs, they can perform the majority of primary metabolisms (described by energy, electron, and carbon source) in addition to specialized processes such as N_2 fixation and H_2 production (Madigan & Jung, 2009). They are tolerant to stresses such as high salinity, heavy metals, and toxic

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contaminants (e.g. H_2S), and can grow in aerobic and anaerobic conditions on a variety of carbon and electron sources, including raw waste streams (Madigan & Jung, 2009). PNSB also naturally produce multiple economically valuable products, including biofuels (Gabrielyan et al., 2015; Vasiliadou et al., 2018), bioplastics (Higuchi-Takeuchi et al., 2016; Monroy & Buitrón, 2020; Ranaivoarisoa et al., 2019), and fine chemicals (He et al., 2021; Sasikala & Ramana, 1995; Wang et al., 2012). Furthermore, they are proficient at removing organics from wastewater (Dhar et al., 2023; Lu et al., 2019), and the resulting biomass is valuable as fertilizer (Maeda, 2021; Sundar & Chao, 2022) and feedstock (Delamare-Deboutteville et al., 2019; Hülsen et al., 2018a; Wada et al., 2022). Altogether, these traits make PNSB an extremely attractive target for biotechnological applications compared to current chemical or purely enzymatic methods, which are limited in their lack of self-repair, specific applications, and need for highly specific operating conditions (Asif et al., 2021). Here, we discuss how PNSB can be leveraged for sustainable bioproduction, as well as limitations to their widespread application.

PNSB Have Diverse Metabolic Capabilities

Purple phototrophic bacteria (PPB) are named for their reddish-purple appearance, which comes from the pigments and carotenoids produced under phototrophic conditions. PPB are separated into purple sulfur (PSB) and PNSB based on their initial characterization in 1932, when one group observed that some PPB could tolerate sulfur and store it intracellularly, while some could not (van Niel, 1932, 1944). It was later found that PNSB could largely tolerate sulfur concentrations <0.5 mM through efflux of oxidized sulfur rather than storage (Hansen & van Gemerden, 1972). Historically, the main attraction of PPB has been as a model for expanding our physiological and biochemical understanding of photosynthesis under anoxygenic conditions (Madigan & Jung, 2009). More recently, this focus has expanded to include the potential for PPB in biotechnological applications–specifically PNSB, which can utilize a variety of electron donors and acceptors and are relatively easy to grow under laboratory conditions compared to the sulfur-requiring PSB (Madigan & Jung, 2009). (This review will focus on PNSB, but where studies do not denote the specific purple bacteria or use a mixed consortium of PNSB and PSB, the term PPB will be used) Although many PNSB species and consortia have been identified, research largely focuses on a few well-characterized "model" species: *Rhodopseudomonas palustris* (*R. palustris*), *Rhodospirillum rubrum* (*R. rubrum*), *Rhodopseudomonas capsulatus* (a.k.a. *Rhodobacter, R. capsulatus*), and *Rhodobacter sphaeroides* (a.k.a *Cereibacter*, *R. sphaeroides*). As mixotrophs, most PNSB species can switch metabolic modes between primary metabolisms, with species-specific differences in efficiency and utilization. This gives them a competitive edge over more metabolically specialized species in non-uniform environments such as waste streams and aquatic environments, where carbon source and light availability may be inconsistent. Additional considerations, such as nitrogen source or oxygen presence, will also have an impact on the preferred mode, but under light-available anaerobic conditions, PNSB will generally perform photoheterotrophy. Fig. 1 provides a schematic overview of the four primary metabolisms PNSB can perform (Li et al., 2022).

Photoheterotrophy

This mode utilizes light for energy generation and organics as a carbon source. During anoxygenic photosynthesis, light is used to excite electrons in the photosystem complexes, which are then passed to the quinone pool and used to generate a proton gradient to produce adenosine triphosphate (ATP) via ATP synthase. Since this process is cyclic (electrons return to the primary donor, bacteriochlorophyll), no water is consumed nor oxygen produced (Adessi et al., 2021). Organic carbon sources include easily metabolized inputs such as organic acids, like malate or succinate, as well as fatty acids, amino acids, carbohydrates, alcohols, and even some aromatic compounds (Asif et al., 2021). The citric acid cycle (also known as tricarboxylic acid cycle) has readily accessible entry points for malate, acetate, succinate, fumarate, and pyruvate, thus making these organic acids the preferred source in many situations as they do not require further energy-intensive degradation pathways before use (Madigan & Jung, 2009). In the case of acids with a higher degree of reduction relative to biomass (4 mol e^- mol^{-1} C), an electron acceptor such as CO_2 or dimethyl sulfoxide (DMSO) is required to allow for growth (Alloul et al., 2023; Richardson et al., 1988). Uniquely, in addition to being able to use organics as an electron source, PNSB can utilize inorganic substances such as minerals (see next section) to obtain their reducing equivalents.

Photoautotrophy

This mode utilizes light for energy generation, CO_2 for carbon, and inorganic substances as an electron source. PNSB possess a functional Calvin-Benson-Bassham cycle (CBB) that is used to both fix carbon for use in the cell, and as a means of consuming excess reducing power. Inorganic substances that can serve as an electron source include reduced metals (e.g. Fe^{2+}) (Ehrenreich & Widdel, 1994), H_2 (Tsygankov & Khusnutdinova, 2015), sulfur compounds (Dahl, 2008), nitrite (Griffin et al., 2007), and bioelectrochemical systems where a cathode directly supplies electrons (Manchon et al., 2023a). This last method is referred to as electrotrophy and is discussed further below.

Chemoautotrophy

This mode utilizes the oxidation of an external electron donor for energy generation and reducing power and CO_2 for carbon. The electron donor is inorganic (e.g. H_2, sulfur, nitrogen compounds), and can contribute to energy via oxidative phosphorylation (i.e. respiration) wherein the electrons are transferred to carriers in the electron transport chain (ETC) until their final transfer to an electron acceptor (Klamt et al., 2008). In aerobic conditions, this acceptor is O_2, while under anaerobic conditions there are several possible oxidants (e.g. DMSO, trimethylamine N-oxide, sulfate, nitrate) (Richardson et al., 1988; Sajitz et al., 1993).

Chemoheterotrophy

This mode utilizes the oxidation of electron donors (organic or inorganic, see prior section) for energy generation and reducing power, and organic substances as a carbon source. In the case of an organic source, sugars can be fermented to support growth, although extensive growth may require an additional accessory oxidant, such as DMSO (Madigan & Jung, 2009). The organic substance used for carbon can also serve as an electron donor; however, inorganic donors can also be used, resulting in a mixotrophy where both organic and inorganic sources are utilized.

Nitrogen Fixation

(Masepohl, 2017) All PNSB species are diazotrophs, meaning they can grow without an external source of fixed nitrogen due to their possession of nitrogenases. These metalloenzymes require 16 moles of ATP to fix one mole of N_2, which also produces an obligatory mole of H_2. In the absence of N_2, the nitroge-

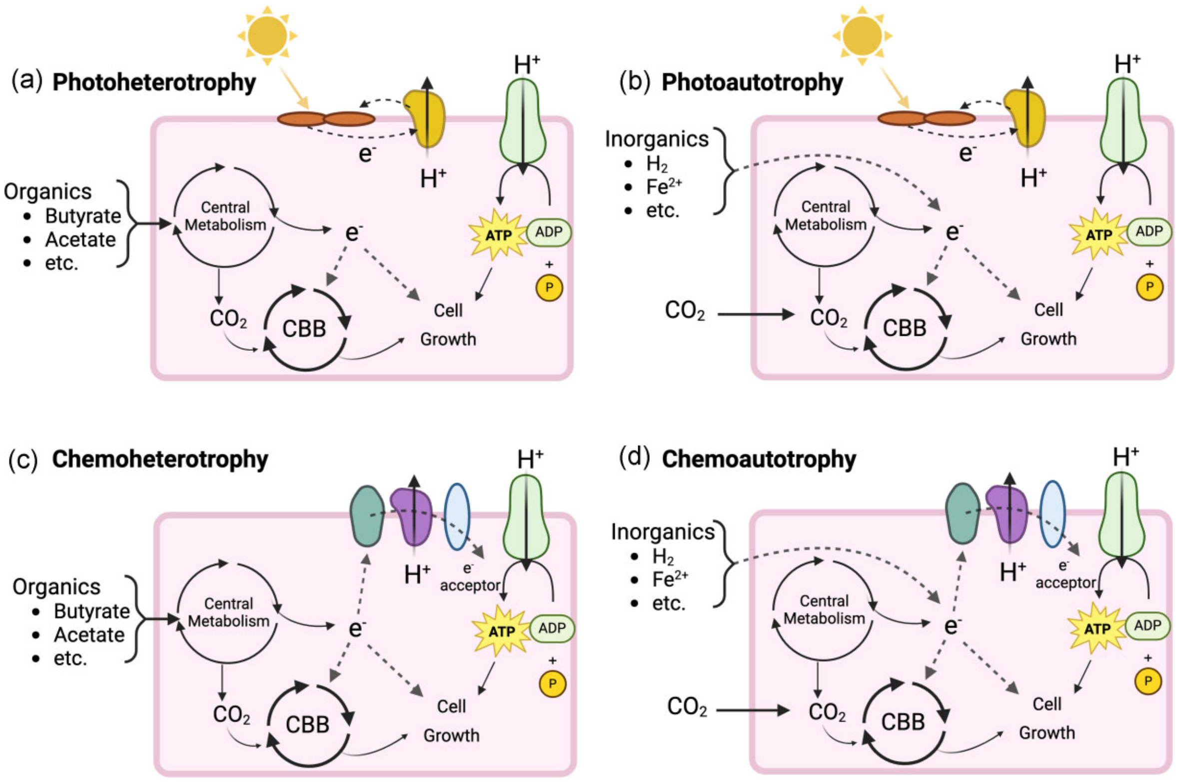

Fig. 1. The four primary metabolisms of PNSB: (A) Photoheterotrophy utilizing organic sources for electrons and carbon, and light for energy, (B) Photoautotrophy utilizing inorganic electron sources, carbon dioxide for carbon, light for energy, (C) Chemoheterotrophy utilizing organic sources for electrons, carbon and energy, and (D) Chemoautotrophy utilizing inorganic sources for electrons and energy, and carbon dioxide for carbon. In A and B, a simplified photosynthetic electron transport chain (ETC) cycles electrons though the reaction centers (orange) and a cytochrome bc_1 complex (yellow). In C and D, a simplified respiratory ETC directs electrons through NADH dehydrogenase (dark green), a cytochrome bc_1 complex (purple) and a cytochrome cbb_3 oxidase(blue). ATP synthase (light green) uses the proton gradient generated by the ETC to make ATP.

nase can still function purely as a hydrogenase, consuming protons and producing H_2 gas. So far, all currently characterized nitrogen-fixers possess a molybdenum-dependent nitrogenase, but some PNSB species have additional vanadium-dependent and/or iron-dependent nitrogenases, such as *R. palustris* (Larimer et al., 2004), which possesses all three. Although they are less efficient than the Mo-enzymes, they can also contribute to H_2 production.

Electrotrophy

(Logan et al., 2019) This ability involves extracellular electron transfer (EET), wherein a microbe can either consume electrons from an external donor (electrotroph), deposit electrons onto an external electron acceptor (electrogen), or both, as is the case with PNSB (Grattieri, 2020; Lovley & Holmes, 2022). This transfer can be facilitated directly via contact between the electron source and factors on the cell surface (e.g. cytochromes), or indirectly using external and internal redox mediators such as H_2 (Shi et al., 2016). For PNSB, viable electron sources include electrodes (both cathodic and anodic), ferrous minerals, and other microbes (Grattieri, 2020).

PNSB Have a Wide Range of Biotechnological Applications

Intact PNSB, as well as their derived products, have multiple applications across a broad range of sectors, including agricultural, municipal, and commercial. A summary of their applications, as well as the current chemical and biological alternatives, can be seen in Table 1.

Wastewater Treatment and Resource Recovery

Water is critical for all aspects of life, ranging from irrigation to hydroelectric power to drinking water. In 2015, the U.S. alone used 322 billion gallons per day, 87% of which was freshwater (Center for Sustainable Systems, University of Michigan, (2023). This results in the production of billions of gallons of wastewater, which includes sources such as sewage, industrial aqueous waste (i.e. brewery, manufacturing, pulp, etc.) and irrigation runoff (Ahuja, 2014). Wastewater requires further chemical and physical treatment before reuse or release into the environment, however many countries discharge wastewater from municipal and industrial treatment plants directly into water streams with little to no treatment (UN Habitat and WHO, 2021). This aquatic pollution is not only damaging to the environment and human health, but prevents the reuse of valuable freshwater (Wear et al., 2021). Furthermore, it prevents the potential conversion of organic substances and otherwise toxic pollutants into valuable products, commonly referred to as resource recovery. In order to support a CE, we need to focus on the recovery of energy, nutrients and water by using energy-producing or net energy-neutral treatment methods such as anaerobic digestion (AD) (Batstone & Virdis, 2014).

Currently, several techniques are employed to treat wastewater, broadly categorized into physical, chemical, and biological

Table 1. Summary of the Biotechnological Applications of PNSB With Standard Chemical Alternatives, a Description of the Genes Involved in the Biological Method Utilized for That Application, and Examples of These Applications in PNSB

Biotech application	Chemical methods	Enzymes/genes involved	Biological methods	PNSB examples	References
Biofuels	Pyrolysis, gasification, liquefication (Jain et al., 2022)	Extracellular degradation	Anaerobic digestion (AD) (Ambaye et al., 2021; Shahid et al., 2021)	Nutrient recovery and CH_4 production in AD, biohydrogen production	(Bai et al., 2021; Gabrielyan et al., 2015; Segura et al., 2023; Silva et al., 2019; Vasiliadou et al., 2018)
Wastewater (WW) treatment	Electrochemical oxidation (Rashid et al., 2021)	Oxidoreductases (peroxidases) (Al-Maqdi et al., 2021; Thulasisingh et al., 2023)	Phototrophic microbes, anaerobic digestion (Machineni, 2019; Sharma et al., 2023)	Removing organics from agri-industrial, municipal, fuel-synthesis WW	(Bunraksa et al., 2020; Dalaei et al., 2019; Hülsen et al., 2019; Hülsen et al., 2018a; Hülsen et al., 2018a; Wada et al., 2023)
Fertilizer	Urea, diammonium phosphate (Shanmugavel et al., 2023)	Nitrogenase (*nif* cluster), phosphatase, xylanase (Gianfreda & Ruggiero, 2006; Piotrowska-Długosz, 2019)	Application of dead or living microbes, PGPS (Stamenković et al., 2018)	Improving rice N_2 content, improving corn yield	(Elbadry et al., 1999; Gamal-Eldin & Elbanna, 2011; Harada et al., 2005; Iwai et al., 2022; Maeda, 2021; Nunkaew et al., 2014; Sakarika et al., 2020; Sakpirom et al., 2017; Sundar & Chao, 2022; Wang et al., 2021)
Bioplastic	Cellulose acetate from agricultural, vegetable waste (Farid et al., 2021), ring opening polymerization (Medeiros Garcia Alcântara et al., 2020)	*phbABC* (Choi et al., 2020)	Phototrophic microbes	Polyhydroxybutyrate production on WW	(Brandl et al., 1991; Cabecas Segura et al., 2022; Carlozzi et al., 2022; Higuchi-Takeuchi et al., 2016; Monroy & Buitrón, 2020; Touloupakis et al., 2021)
Single cell protein	N/a	Amino acid synthesis pathways	Harvest fungi, yeast, algae, bacteria after growth on waste stream (Koukoumaki et al., 2024)	Aquaculture feed	(Alloul et al., 2021b; Alloul et al., 2021c; Delamare-Deboutteville et al., 2019; Hülsen et al., 2022; Hülsen et al., 2018a; Patthawaro & Saejung, 2019; Rashid et al., 2022; Saejung & Ampornpat, 2019; Wada et al., 2022, 2023)
Fine Chemicals [coenzyme Q10 (CoQ), carotenoids (Crt)]	Crt: plant tissue solvent extraction, electrolysis (Sundararajan & Ramasamy, 2024) CoQ: isoprenoid catalyzed coupling, tissue extraction (Shukla & Dubey, 2018)	Crt: *Crt* cluster (Rodriguez-Concepcion et al., 2018; Takaichi, 2009) CoQ: Shikimate and MEP pathway, *ubi* cluster	Crt: Growth of photosynthetic microbes (Pirwitz et al., 2015) CoQ: Microbial (with high CoQ content) fermentation	CoQ: production on brewery WW, artificial sugar WW, pure cultivation systems	(Soon et al., 2014; Wang et al., 2012; Yu et al., 2021) (He et al., 2021; Zhang et al., 2018; Zou et al., 2019)

treatments. For a thorough review of wastewater and its treatment techniques, see Machineni (2019) and Thulasisingh et al. (2023).

Biological treatments offer a cheaper, less toxic, and more complete treatment of wastewater, especially when combined with physical or chemical methods, pending the usage of appropriate organisms and/or enzymes. Importantly, these methods also allow for the recovery of organic compounds in the wastewater, such as phosphorous or carbon, for usage as fertilizers or precursors for other bioproducts.

Sharma et al. (2023) recently reviewed these biological treatments as well as some of the microbes that perpetrate them, ranging from fungi (Assress et al., 2019) to patented bacteria (Villela et al., 2019). However, several barriers prevent a more widespread application of these treatments—namely, high capital and operational costs, including the maintenance of specific growth conditions and removal of the "sludge" generated from microbial growth (Sravan et al., 2024). To make the treatment process cheaper and more sustainable, photosynthetic microbes are being considered for their ability to use the free, effectively limitless source of sunlight (Lu et al., 2019). Microalgae are one candidate, but are limited by their high light requirement, while chemoheterotrophs often require aeration. On the other hand, PNSB can grow even under light-limited conditions and have no oxygen requirement. Additionally, they can consume the waste organic material and convert it into a variety of useful products such as biofuels or bioplastics. Furthermore, their superior ability to assimilate organic compounds, as well as phosphorous and nitrogen allow the microbes themselves to become a concentrated source of nutrients which can be used as a source of protein or fertilizer, while simultaneously preventing these organic inputs from contaminating the environment and encouraging harmful algal blooms (Capson-Tojo et al., 2020). In short, they can both consume waste and neutral inputs and produce valuable products from these inputs, effectively re-introducing these resources into the CE.

PNSB have demonstrated success in removing organic material from a variety of wastewaters, making them promising candidates for widespread application. For example, saline wastewater, which includes seawater used for industrial processes or toilet-flushing, can be difficult to treat due to the high salt and sulfate concentrations, which can lead to the formation of toxic sulfides. However, PNSB can not only withstand these conditions, but also adapt much quicker without standard stepwise adaptation: Hülsen et al. demonstrated that a PPB-enriched culture could rapidly adapt to high-salt conditions in saline wastewater to achieve biomass yields of 0.8 g COD g $COD^{-1}{}_{fed}$ [chemical oxygen demand (COD) is a measurement of the oxygen required to oxidize organic matter, where 1.0 g COD g $COD^{-1}{}_{fed}$ would indicate complete conversion of waste (fed) COD to biomass] (Hülsen et al., 2019). Here and elsewhere in this review, PPB-enriched refers to a mixed culture typically from a wastewater source that has been treated to enrich levels of PPB, often containing significant levels of PNSB among other bacterial species. The Fischer–Tropsch process is used to generate liquid fuel in the form of hydrocarbons from carbon monoxide and hydrogen, but since the resulting wastewater lacks fixed nitrogen, it is difficult to treat biologically. However, like diazotrophs, PNSB can grow on this wastewater, achieving up to 70% COD removal despite the stringent growth conditions (Wada et al., 2023).

On domestic wastewater, Hülsen *et al.* showed that a >60% PPB-dominated community provided with 200 mg L^{-1} of ethanol could achieve nutrient removal to discharge limits (<50 mg COD L^{-1}, 5 mg N L^{-1}, 1.0 mg P L^{-1}) (Hülsen et al., 2016). Further, Cerruti et al. found that PNSB enriched from wastewater treatment plant activated sludge could achieve 96% COD removal at a volumetric rate of 1.1 kg COD d^{-1} m^{-3} when grown on synthetic wastewater in a stirred batch reactor setup (Cerruti et al., 2020; Dalaei et al., 2019). In both cases, PPB demonstrates impressive efficiency in recovering waste organic materials, a necessary resource for building new bioproducts to foster the CE.

PNSB also perform well on agricultural wastewater, which can possess even higher organic content than domestic sources and thus requires greater COD removal. When grown on chicken slaughterhouse wastewater, one group found that *Rhodopseudomonas faecalis* and *R. palustris* could remove up to 88% of soluble COD (Bunraksa et al., 2020). Another study using poultry and red meat processing wastewater saw PNSB biomass yields above 0.75 g COD g $COD^{-1,}$ with high assimilation of nitrogen and phosphorous (Hülsen et al., 2018a). As is discussed in "Fertilizer" section, having a high nitrogen and phosphorous content makes the microbe suitable for use as fertilizer, making these PNSB an upvalued product.

There are a number of challenges associated with the aquatic, phototrophic growth and recovery of PNSB biomass that apply to the majority of PNSB applications discussed in this work, including wastewater treatment. Capson-Tojo et al. composed a full review of the challenges associated with PPB wastewater treatment but currently, the most costly issue is the light requirement (Capson-Tojo et al., 2020). As has been established with microalgae technologies, it is difficult to design a reactor that allows efficient light delivery while allowing high biomass accumulation. Using PNSB for resource recovery is one way to offset these costs, as is using natural sunlight instead of artificial illumination (Sepúlveda-Muñoz et al., 2023). However, to date, very few studies have explored the use of natural light; unlike aerobic microalgae which are naturally found in open air pond setups, PNSB often require an anaerobic environment to maintain dominance as aerobic conditions allow for other heterotrophs to grow. Nonetheless, Alloul *et al.* found that PNSB abundance in an open raceway reactor could be increased from 50% to 67% to >88% by limiting the organic availability to only what could be consumed during the light period. Combined with a lack of stirring (aeration) at night, these measures effectively suppressed non-PNSB growth while still allowing protein production up to 0.2 g protein L^{-1} day^{-1} (Alloul et al., 2021a) Harvesting PNSB biomass after resource recovery also presents an issue with few optimal solutions as the planktonic cells are dilute and difficult to capture, especially on a large scale. One way to concentrate the cells is by encouraging biofilm growth, which focuses biomass in one location and can even improve characteristics such as crude protein content and ease of resource extraction (Hülsen et al., 2020b; Ozkan et al., 2012). It should also be noted that despite achieving higher COD conversion efficiencies compared to aerobic heterotrophs (AHs), PNSB tend to have a slower growth rate, especially under autotrophic conditions. This can be somewhat improved using reactor design, but ultimately is considered a tradeoff in microbial species selection (Alloul, Cerruti, et al., 2021a; Zhang et al., 2024).

The exceptional abilities of PNSB to recover resources from a variety of wastewaters combined with their unique metabolic capabilities make them extremely attractive candidates for microbial wastewater treatment. Although PNSB face several challenges related to phototrophic growth, the inherent value of the biomass produced will assist in offsetting costs as more groups look to focus on resource recovery as part of wastewater treatment.

Biofuel Production

With an increasing global population comes an increase in energy demand. Although coal, natural gas, and petroleum were reported to meet 80% of the global energy demand in 2014, fossil fuel-based products are neither environmentally friendly nor sustainable and will struggle to meet increasing demand in the near future (*WEO-2015 Special Report*, 2015). Instead, the global community is looking to biofuels such as bioethanol, biodiesel, biohydrogen, and biogas. The newest generation of biofuels relies on a net carbon-neutral microbial production process achieved by reducing GHG emissions and absorbing CO_2 while the biomass is alive. In the last 10 years, the global capacity for bioenergy generation has nearly doubled to 144 GW, constituting about 5% of the total renewable energy capacity (*Renewable Capacity Statistics 2022*, 2022). However, the optimization of biomass-derived biofuels and energy production is still in its infancy, and this number is predicted to grow as improvements are made to current processes.

Ambaye et al. extensively reviewed the evolution of biofuel production methods over the last 50 years (Ambaye et al., 2021). Briefly, the first generation involved the processing of food crops to produce ethanol and biodiesel (Naqvi & Yan, 2015), while the second generation focused on using lignocellulosic biomass, which is more difficult to degrade (Gautam et al., 2024). The third generation sought to harvest the biomass of microbes to extract biofuels (Maliha & Abu-Hijleh, 2023). Finally, the most recent fourth generation uses genetic modification to enhance the carbon capture/biofuel production abilities of candidate microbes, which combined with the extraction processes of the third generation has produced promising results (Abdullah et al., 2019; Cavelius et al., 2023).

Biohydrogen can be produced via bio-photolysis, photofermentation, or dark fermentation (Teke et al., 2024). Photofermentation is being increasingly studied to improve the sustainability of H_2 production, both alone (using renewable inputs) and together with dark fermentation (more completely processing the organic input). Compared to microalgae and cyanobacteria, which produce H_2 through oxygenic photolysis, PNSB produce biohydrogen via their nitrogenase and some hydrogenase enzymes under anoxic conditions. The hydrogenase function of the nitrogenase persists even in the absence of N_2, as McKinlay et al. observed when H_2 production by *R. palustris* CGA009 increased by 3.5-fold under N_2-starved conditions compared to growth with available N_2 (McKinlay et al., 2014). There have been extensive and diverse efforts to improve H_2 production in PNSB, only a few of which we can highlight here (Gupta et al., 2024). Several groups have focused on substrate utilization, specifically dark fermentation effluent (DFE), which is the residue rich in volatile fatty acids (VFAs) remaining after the fermentation of organic matter, such as an organic waste stream, under no-light conditions. DFE has been successfully used as a substrate for *R. sphaeroides* growth and H_2 production up to 256 mL H_2/g COD (COD is a measurement of the oxygen required to oxidize organic matter) (Ghimire et al., 2016). DFE also supported H_2 production up to ~100 mL in a 1.5 L bioreactor with *R. capsulatus,* although the addition of lactose was required to encourage fermentation (Silva et al., 2019). Multiple studies have also employed DFE from axenic cultures to support PNSB H_2 production, including the hyperthermophilic *Thermotoga neopolitana* (9.4 mol H_2/mol glucose) (Dipasquale et al., 2015), skilled fermenter *Lactobacillus amylovorus* (3.1 mol H_2/mol glucose) (Adessi et al., 2018), and *Clostridium butyricum* (11.6 mol H_2/mol sucrose) (Lo et al., 2010). Alternate strategies to improve H_2 production include the addition of nanomaterials (Bosu & Rajamohan, 2024) as well as focusing light emission spectra (Bosman et al., 2023; Tiang et al., 2024). PNSB can also improve the sustainability of H_2 production using electrotrophic abilities: when growing a mixed culture of PPB enriched from wastewater with malic acid and a cathode electron donor, researchers found the culture could achieve comparable H_2 production to non-cathodic growth while fixing all available CO_2 (Vasiliadou et al., 2018). While the yields measured in this study (0.11 L H_2/g malic acid) are still lower compared to other PNSB studies, this is a novel application with plenty of room for optimization. However, it should be noted that many dark fermentation setups outperform the best pilot autotrophic setups in total H_2 yield per g biomass without major modifications.

Another biofuel for consideration is biogas, which is largely composed of methane (40–70%), carbon dioxide (25–45%) and trace amounts of N_2, O_2, and H_2S. The higher the methane content, the more ideal the biogas as it requires less "cleaning" to remove contaminants before drop-in to existing natural gas frameworks (Calbry-Muzyka et al., 2022). One way to produce biogas is via anaerobic digestion (AD), which involves a community of microbes performing hydrolysis, acidogenesis, acetogenesis, and finally methanogenesis to degrade waste organic matter (Bhatt & Tao, 2020). Finding a suitable organic matter for feedstock can be especially challenging, as an ideal substrate would be low-to-no cost to produce or obtain while possessing enough nutrients to support AD and biogas production. In this sense, PNSB biomass makes for an attractive input, as it can be produced on renewable inputs like sunlight and CO_2, as well as organic waste streams, where they demonstrate remarkable ability to recover nutrients (see "Wastewater Treatment" and "Single Cell Protein" sections) (Hülsen et al., 2020a). However, due to their high protein content and inherent ability to survive under anaerobic conditions (as compared to aerobic microbes from waste streams), PNSB will likely require pre-treatment to enhance digestibility. For example, Segura et al. showed that PPB mixed cultures enriched from wastewater when thermally treated at 180°C for 15 min before being added to an anaerobic digester achieved significantly higher methane production (307 vs. 177 L methane/kg volatile solids) and volatile solids destruction (75% vs. 34%) compared to the no treatment control at 20 days hydraulic retention time (Segura et al., 2023). Despite this improvement, the results achieved to date still fall short of achieving positive energy recovery in the scheme of growing the biomass, digesting it, and recovering the resulting energy (Hülsen et al., 2020a). Intriguingly, *R. palustris, R. rubrum*, and *R. capsulatus* have also been found to produce small amounts of CH_4 directly via their iron nitrogenase during N_2 fixation. However, although the amount produced by *R. palustris* is sufficient to support a co-culture with obligate CH_4 consuming *Methylomonas* sp., it is unlikely to be a significant source of methane as a biofuel (Zheng et al., 2018).

As for other biofuels, Doud et al. achieved the conversion of butyrate to *n*-butanol in *R. palustris* CGA009 by introducing *adhE2*$_{824}$, a codon optimized aldehyde dehydrogenase from *Clostridium acetobutylicum* ATCC 824 (Doud et al., 2017). The strain could produce up to 1.5 mM *n*-butanol, but required stressful growth conditions that limited channeling of electrons through alternate production pathways. Bai et al. went a step further by introducing a five-gene cassette used for *n*-butanol production in *E. coli* into *R. palustris* TIE-1 to produce *n*-butanol under heterotrophic, autotrophic and electrotrophic growth. They further found that by removing *nifA* to prevent nitrogen fixation (an alternate electron-consuming pathway), the strain could produce up to 4.98 ± 0.87 mg/L *n*-butanol under photoheterotrophic conditions, more than double that of the cassette alone (Bai et al., 2021). Again, although these values are much lower than other butanol production chasses [i.e. >500 mg/L in engineered *al.oli* (Atsumi et al., 2008)], the value of using PNSB lies in their ability to utilize renewable inputs and thus be employed in systems like bioelectrochemical synthesis (see Avant-garde Technologies).

PNSB are part of a broad range of candidates used for bioenergy, but benefit from being able to use a wide range of renewable inputs and grow under harsh conditions such as that of wastewater. Although PNSB demonstrate success as feedstock for AD or producing biohydrogen, their use for bio-energy is comparatively under-explored. Further research is required to better understand the limitations and areas of optimization for using living or dead PNSB biomass for bio-energy production.

Fertilizer

Improving agricultural output is critical for sustaining the ever-increasing global population. Large areas of the world are already beginning to experience food limitations, which will only be compounded in the coming decades (FAO, 2017). To encourage rapid and healthy growth of food crops, fertilizers are often used to provide necessary nutrients not readily available in soil. Fertilizers typically contain nitrogen, phosphorous, and potassium (NPK), often with additional growth-promoting compounds. A common method of fertilization is to add NPK in the form of readily accessible inorganic compounds like urea (46% N) or diammonium phosphate (18% N, 46% P_2O_5) (*Corn Nutrition 101*| *Crop Science US*, 2024). However, they are frequently applied above the limits of nutrient absorption by the plant, leading to excess nutrients washing off into waterways and causing eutrophication, or contributing to GHG emissions (Shanmugavel et al., 2023; Vejan et al., 2021). Organic fertilizers such as manure can also cause nutrient leaching, but generally improve the health of the soil in terms of fertility, water retention, and promoting microbial communities. However, due to its slower effect on growth, it often requires mixing with inorganic fertilizers, and long-term use can lead to heavy metal accumulation (Diacono & Montemurro, 2010; Lu et al., 2024). Plus, it is estimated that the production and use of manure and synthetic nitrogen fertilizers account for ~5% of global GHG emissions (Gao & Cabrera Serrenho, 2023). Alternatively, bio-fertilizers, which employ live or dead microbes to promote plant growth, appeal directly to the microbial communities in the soil (Stamenković et al., 2018). By providing nutrient-rich biomass or live members capable of performing biogeochemical cycling, this method avoids run-off and soil exhaustion while still providing benefits to the plant (Spanoghe et al., 2020). Photosynthetic microbes are particularly attractive for use as bio-fertilizer because they are cheap to produce when grown photoautotrophically and can achieve high density depending on the species (Lee et al., 2021).

Microbial cells can contribute to the fertilization of soil in three major ways: (a) directly, by providing NPK as dead or decaying cells, (b) indirectly as living cells that perform nutrient acquisition (i.e. N_2 fixation), or (c) in the form of extracted plant-growth promoting substances. As thoroughly explained by Sakarika et al. (2020), PNSB can serve in all three methods. First, as dead or decaying biomass, they have a favorable NPK content (8.5/2.4/0.5% in dry weight, *Rhodobacter* sp.) (Sakarika et al., 2020). PNSB are particularly rich in phosphorous compared to other photosynthetic organisms (1.3% in microalgae) owing to their ability to accumulate polyphosphate, but their low potassium content may require supplementation (Lai et al., 2017). Despite this, Spanoghe et al. found that dried *Rhodobacter* sp biomass applied to parsley resulted in similar height and fresh weight compared to a reference organic fertilizer (Spanoghe et al., 2020). Morey-Yagi *et al.* also found that applying lysed and dried *R. sulfidophilum* biomass to Japanese mustard spinach yielded similar growth and dry weight to mineral fertilizer, although twice the amount of biomass was required compared to the mineral fertilizer (Morey-Yagi et al., 2024). Although both studies achieved similar performance to commercial fertilizers, PNSB has the production benefit of growth on negative value waste streams, making it a potentially better candidate for the CE compared to traditional organic fertilizers. However, the challenges of scaling up culture and addressing the additional energy and economic costs for transportation and storage make it difficult to replace mineral fertilizers currently.

Alternatively, before dead biomass contributes to soil fertilization, living cells can fix nitrogen to ammonia and actively chelate phosphorous for use by the plant. Importantly, some PNSB species can fix N_2 under microaerobic conditions, allowing for a broader range of environments where they can be applied (Larimer et al., 2004). Several groups have already demonstrated the successful application of PNSB in the microaerobic conditions of rice paddies. One group found that inoculation with *R. capsulatus* resulted in similar biological mass yield and unhulled rice grain yield compared to the application of chemical nitrogen fertilizer at 50% of the recommended nitrogen rate (4.11 t ha^{-1} vs. 4.0 and 10.565 t ha^{-1} vs. 10.233, respectively). Importantly, they saw statistically equivalent yields between 100% and 50% chemical nitrogen fertilizer with *R. capsulatus* inoculation, suggesting that chemical fertilizer usage can be reduced without impact to yield (Gamal-Eldin & Elbanna, 2011). Harada et al. saw a similar result, with an up to 21% increase in rice grain yield when they fertilized using rice straw inoculated with *R. palustris* (Harada et al., 2005). However, in both cases, PNSB inoculation alone had limited effects on plant growth and yield, although its addition increases the usage efficiency of synthetic nitrogen fertilizers by decreasing the quantity of fertilizer required to achieve a set yield (Sundar & Chao, 2022). In an aerobic context, tomato plants inoculated with *Rhodopseudomonas sp.* KL9 showed increased fruit weight, size and lycopene content (Lee et al., 2008). Another group found that peanut plants treated with an inoculum of *R. palustris* ISP-1 saw a 5-year average yield increase of 12.5% compared to conventional fertilizer (Wang et al., 2021). Altogether, these studies demonstrate not only the potential of PNSB to act as a living fertilizer comparable to chemical nitrogen fertilizer, but also the ability of PNSB to be applied across a wide range of environments—a necessary trait when attempting to develop an alternative to the widespread conventional fertilizers. A major concern with the use of living microbes is their shelf life and, by extension, required storage conditions. To the authors knowledge, no data on living PNSB shelf life is available, and only one study on dried biomass shelf life was found, which showed that *Rhodobacter* sp. dried biomass had no net decrease in total solids or nitrogen content after 91 days of storage at 20°C (Spanoghe et al., 2020). Contamination is another concern that directly impacts shelf life; fortunately, PNSB can be selected for using infrared radiation and/or anaerobic growth conditions to reduce the chances of a competing contaminant (Yu et al., 2021). However, further studies will be required to determine the shelf life of living PNSB inoculums under relevant transportation and storage conditions.

Finally, PNSB are reported to produce the plant growth-promoting substances indole-3-acetic acid (IAA) and 5-aminolevulinic acid (ALA). IAA and ALA belong to a class of plant hormones known as auxins that are responsible for regulating everything from root development to fruit maturation. Specifically, IAA plays important roles in plant growth processes and stress response, while ALA has been demonstrated to improve plant growth by enhancing stress tolerance. Both IAA (Piotrowska-Niczyporuk et al., 2018; Takshak & Agrawal, 2017) and ALA (Wang et al., 2023) have been extensively demonstrated to improve plant growth parameters such as stress recovery and crop yield. Thus, it can be expected that production by fertilized microbes could enhance plant growth as well. *R. palustris* in particular is skilled at producing these compounds, with one isolate from a rice paddy field achieving 3.62 mg/L of IAA and 4.11 mg/L of ALA under microaerobic conditions (Sakpirom et al., 2017). Indeed, this same species was reported to produce increased ALA when inoculated into rice fields, and ultimately improved plant growth (Nunkaew et al., 2014). It should be noted that at high concentrations, IAA can become inhibitory to root development and growth, so a lower IAA-producing strain may be favored instead (Sakpirom et al., 2017). By modulating the production rates of these strains to maximize agricultural output, it may be possible to generate a more suitable strain for all-around use, but further experimentation is required.

PNSB demonstrate suitability for use as fertilizer as dead or living biomass, as well as via their derived compounds, for a range of plants and growing conditions. Although specific research will be required to determine the compatibility of PNSB species to plant species, the field already shows promising results for achieving commercial levels of growth using supplemented PNSB. Replacing the demand for environmentally damaging mineral fertilizers with biological ones, even partially, will greatly contribute to improving the sustainability of global agricultural practices in the future.

Polyhydroxyalkanoate (PHA) Production

Modern petroleum-based plastics are favored for their thermal plasticity and low crystallinity, which makes them useful in everything from food packaging to clothing. However, they are extremely resistant to degradation, and their continued use over the last seventy years has resulted in significant environmental pollution. Microplastics can be found in waterways, soils, marine animals, and those that consume them, including humans. Landfills are quickly running out of space and burning the plastic only releases more GHGs (Farid et al., 2021). To support the CE and prevent further environmental damage, a sustainable replacement material with similar properties to petroleum-based plastics is urgently needed. This has led to increasing interest in a microbially produced polymers called polyhydroxyalkanoates (PHAs). PHAs are polyesters with variable-length hydrocarbon side chains (Fig. 2). C3–C5 short chain length (SCL) PHAs tend to be stiffer, while C4–C16 medium chain length (MCL) PHAs are more elastic. PHAs can also be co-polymers composed of multiple types of monomers, which can improve traits like brittleness, stiffness and melting point (Choi et al., 2020). Polyhydroxybutyrate (PHB), in particular, is a popular SCL-PHA that is easy to produce, with comparable thermal and mechanical characteristics to polypropylene (Nanda et al., 2022). PHAs already have functional applications in disposable packaging and also have the potential to be used as biodegradable implants, drug carriers, and in tissue engineering (Bourtoom, 2008; Choi et al., 2020).

PHAs can be produced via several methods: they can be chemically synthesized using a metal catalyst and an initiator such as alcohol to perform ring opening polymerization on cyclic ester monomers (Tang & Chen, 2018). However, the harsh reagents required and high cost make this challenging to scale-up. Alternatively, pure enzymatic production requires a large amount of synthase, as well as stereospecific active form monomers; both can be difficult and expensive to produce and purify (Thomson et al., 2010). Furthermore, the process of polymerization releases CoA, which has a positive feedback inhibitory effect on the enzymes when it is not recycled *in vitro* (Zou et al., 2017). Due to the difficulties of these methods the preferred industrial method is largely biological. PHAs are naturally generated by many microbes as a carbon storage molecule in response to excess carbon or energy, typically under nitrogen or phosphorous-limited conditions (Vicente et al., 2023). The polymer is generated from acetyl-CoA and varying-length fatty acid precursors, thus requiring at least a thiolase, reductase, and synthase to be produced. PHB, for example, is produced using three enzymes: PhaA (β-ketothiolase), PhaB (acetoacetyl-CoA reductase), and PhaC (PHB synthase) (Montiel-Corona & Buitrón, 2021). There are many more enzymes involved in the regulation of PHA production and pathway-dependent enzymes for the polymer carbon source, including amino acid biosynthesis, glycolysis, and β-oxidation (see Choi *et al.* 2020 for a detailed list).

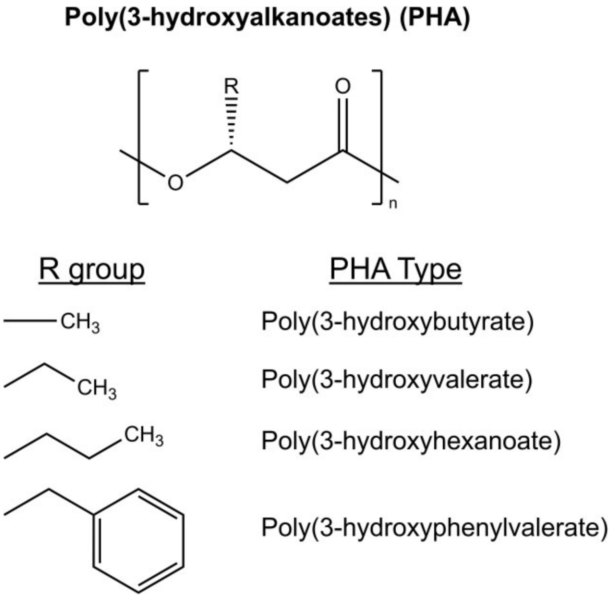

Fig. 2. Generic chemical structure of poly-hydroxyalkanoate (PHA) and example PHA types with their respective side groups (R). For a comprehensive list of PHA types, refer to Choi et al. (2020).

Ralstonia eutropha H16 (a.k.a. *Cupriavidus necator*) is widely considered the hallmark PHA producer, but several species have been found to perform much better in production (Reinecke & Steinbüchel, 2009). The *Pseudomonas* genus offers the ability to grow on diverse carbon sources (Mozejko-Ciesielska et al., 2019), while *Bacillus* can offer dry cell weight yields above 50% (Martínez-Herrera et al., 2023). Cyanobacterium *Synechococcus* sp. MA19 can even achieve PHB production under photoautotrophic conditions (Nishioka et al., 2001). An ideal PHA producer to support the CE would be able to achieve high production rates using sustainable low-value inputs to both reduce cost and environmental burden. PNSB offer the ability to support the CE by using both light *and* waste organic materials, rather than the expensive pure carbon sources required by other species. PNSB can also be genetically enhanced to compete or outperform an engineered non-PNSB chassis.

Many PNSB species have demonstrated the ability to produce PHA under a range of growth conditions, capitalizing on their unique metabolisms. Organic waste streams often have a mix of fatty acids, so a candidate production strain must be able to utilize a variety of these alkanoic substrates to maximize production. Brandl *et al.* found that *R. rubrum* produced PHA on all *n*-alkanoic acids as the sole carbon source under phototrophic conditions, reaching 20% cell dry weight (cdw) on 60 mM butyrate (Brandl et al., 1989). This same group also found that *R. sphaeroides* grown on acetate reached 500 mg PHA/L at 65% cdw, although the authors remarked that this species seemed to have limited flexibility in forming co-polymers compared to *R. rubrum* (Brandl et al., 1991). As mentioned above, PHA co-polymers can have improved traits compared to mono-polymers which makes them desirable for practical application; fortunately PNSB are quite capable of producing them. Carlozzi *et al.* demonstrated that *Rhodovulum sulfidophilum* could achieve up to 330 mg/L of the copolymer PHB-co-3-hydroxyvalerate when grown on lactate on a light/dark cycle (Carlozzi et al., 2022). Furthermore, as a marine bacterium, *R. sulfidophilum* can grow on high salt substrates such as sterilized sea water, which can further reduce costs. Higuchi-Takeuichi et al. demonstrated that nine different marine PNSB species could achieve PHA and co-polymer production, most notably *Rhodovulum visakhapatnamense* reaching 300 mg PHA/L and *R. sulfidophilum* at 250 mg PHA/L on nitrogen-limited media with acetate (Higuchi-Takeuchi et al., 2016). PNSB already demonstrated the ability to grow on wastewater (see section "Wastewater Treatment"), with several groups focused on resource recovery in the form of PHA. Allegue et al. tested the ability of a PPB-enriched culture to grow on the hydrolysate of thermally pre-treated lignocellulosic waste and found that the culture could produce PHB up to 20% cdw (Allegue et al., 2021). Many others turned instead to the DFE of various wastewater sources, which is richer in easy-to-consume VFAs than raw wastewater, and saw significant PHA production as reviewed by Montiel-Corona and Buitron (2021).

Despite the range of carbon sources available for use, PNSB PHA production still faces the main challenges of low PHA production rate and low biomass production. As discussed in "Wastewater Treatment," improving reactor design to encourage higher light efficiency with controlled temperature and stirring can encourage higher biomass accumulation. Limiting nutrient availability and keeping the C/N ratio high can also encourage PHA production. Capitalizing on the unique metabolism of PNSB may also contribute to optimization; indeed, Ranaivoarisoa et al. showed that *R. palustris* TIE-1 could produce PHA under not only photoheterotrophy, but also autotrophic conditions including hydrogenotrophy, ferrotrophy, and electrotrophy (Ranaivoarisoa et al., 2019). Exploring novel chassis PNSB can also yield insight into optimization, as Conners et al. recently demonstrated that the previously unstudied *Rhodomicrobium* sp. could produce up to 44 mg/L PHA under photoheterotrophic growth (Conners et al., 2024). Genetic engineering to hyperactivate PHA production or prevent resource-sharing with other pathways showed great success in other organisms as well as PNSB; Foong et al. employed genome-wide mutagenesis to select for high PHA accumulation and found an *R. sulfidophilum* mutant that reached maximum PHA production 2 days earlier than wildtype (Foong et al., 2022). In a more targeted approach, Ranaivoarisoa *et al.* showed that an *R. palustris* TIE-1 mutant lacking *phaR* produced significantly more PHB during photoheterotrophic growth on butyrate. Intriguingly, they also found that the insertion of RuBisCO forms I and II expressed from a constitutive promoter significantly increased PHB production during autotrophic growth with H_2 in addition to butyrate (Ranaivoarisoa et al., 2023). It is possible that this increase in production is due to an increased ability to fix carbon under autotrophy or process the excess electrons associated with utilization of butyrate (a reduced substrate). However, further research will be required to elucidate the metabolic interplay of PNSB pathways, especially those identified as redox-balancing.

PNSB are natural producers of PHA with the ability to grow on renewable inputs and negative value waste streams under a range of environmental conditions. Their PHA production can be further enhanced via genetic engineering, however current biomass yields and production rates remain too low for practical application. Future research should seek to enhance yields through reactor design and genetic manipulation.

Single Cell Protein (SCP) Production

Despite the growing demand for global food production, the total arable land estimated on Earth remains at 24%, with about half being actively cultivated. This arable land is being degraded through irresponsible agricultural practices and the effects of climate change, which could take decades to reverse (AbdelRahman, 2023). Therefore, it is critical to develop eco-friendly food solutions, such as those that do not require arable land. To solve this issue, scientists have turned to microorganisms. The term "single cell protein" was introduced in 1968 to refer to protein-rich foods derived from the cells of microorganisms (Najafpour, 2007). SCP offers convenience, high yields, and reduced costs through growth on renewable inputs (e.g. sunlight, waste streams), making them an attractive alternative to protein products for the CE (KV, 2022). In fact, several commercial products exist today, most notably the worldwide company Quorn, which produces food products using mycoprotein (Kazer et al., 2023; Ribeiro et al., 2023). Many microbes have been tested for SCP ability, including fungi, yeasts, bacteria, and algae. However, as Koukoumaki et al. (2024) discuss in their recent review, bacteria offer the highest growth rate and range of substrate utilization.

PNSB are stand-out candidates even among bacteria due to their high crude protein content (up to 60% dry weight) with a balanced amino acid profile, and their production of useful additives such as bacteriochlorophyll, carotenoids and ubiquinones (Saejung & Ampornpat, 2019). They also produce a multitude of vitamins, including thiamine (B_1), riboflavin (B_2), biotin (B_6), cobalamin (B_{12}), tocopherol (E), niacin, folic acid, and pantothenic acid (Sasikala & Ramana, 1995). Their robust metabolism allows them to thrive even on unsterilized waste stream inputs, be easily enriched with infrared light, and outcompete common grazers and predators under anaerobic conditions (Wada et al., 2022). To this point, a mixed PPB-enriched culture grown on various wastewaters achieved an average caloric value of 22 MJ/kg volatile suspended solids, nearly double that of conventional protein sources like meat and bonemeal (Batterham et al., 1980; Hülsen et al., 2018b). Shaikh *et al.* utilized the severely nutrient-limited fuel synthesis wastewater (produced during the Fischer–Tropsch process) to support the growth of a mixed culture of PNSB; they found that the culture could reach >35% protein content even with major nutrient (N, P, Mg, and Ca) deficiencies (Shaikh et al., 2023). Patthawaro and Saejung also tested the growth of *R. faecalis* on different animal manures; using 15% chicken manure media, they achieved 525 mg/L protein production with a biomass composition of 62.7% crude protein (Patthawaro & Saejung, 2019). Another group was able to grow *R. faecalis* PA2 directly on undiluted wastewater from a treatment pond, achieving high protein (64.8%) and lipid content (10.6%) with an essential amino acid profile similar to the dietary requirements of penaeid shrimp (Saejung & Ampornpat, 2019).

Although PNSB's nucleic acid content is low relative to the bacterial average (<5% vs. 10–15%), this far exceeds that of traditional protein sources (<0.06%) (Patthawaro & Saejung, 2019). Because of the recommended RNA limit of 2 g/d for humans, this limits human consumption, as well as usage for mammals and birds (Imafidon & Sosulski, 1990). However, aquatic animals can tolerate much higher nucleic acid levels (Carlberg et al., 2018). Multiple studies have demonstrated the success of PNSB as an aquaculture feed additive, although it should be noted that thus far no-one has attempted or achieved growth with PNSB SCP as a sole nutrient source. Delamare-Deboutteville *et al.* found that when feeding Asian sea bass, bulk replacement of fish meal with mixed cultures of PPB at 33% and 66% was both feasible and commercially viable (Delamare-Deboutteville et al., 2019). Another group found that white leg shrimp, when fed a diet with 10% PNSB-derived protein, grew up to 25% larger than the control group and were more resistant to ammonia stress. Beyond protein content, PNSB also produce a number of compounds beneficial for aquaculture: as photosynthetic bacteria, they produce carotenoids, which provide a brighter color to salmon and shrimp (see section Fine Chemical Production). Additionally, some PNSB can produce extracellular proteolytic enzymes, which would assist in removing excess fish feed and keeping tanks clean (Seangtumnor et al., 2018). Uniquely, PNSB have also been found to inhibit the widespread shrimp pathogen *Vibrio parahaemolyticus* reducing both mortality rates of shrimp and the need to apply prophylactic antibiotics that contribute to the rise of antibiotic resistant bacteria (Chumpol et al., 2017).

Unlike the other biotechnologies, one of the biggest hurdles with upscaling SCP production is improving public opinion, especially when produced using wastewater, which is classically associated with uncleanliness. As such, it is important to emphasize the probiotic abilities of PNSB and their success in aquaculture use, as well as their lack of toxins. Other considerations such as maintaining consistent composition and enhancing total biomass production will depend on the waste stream or carbon source selected for use and reactor design; both are being actively explored to enhance not just SCP but other biotechnological applications of PNSB (Rashid et al., 2022; Wada et al., 2022).

SCP is a promising sustainable alternative to conventional food sources that would support the CE. PNSB are strong candidates for SCP with their high protein content, favorable nutrition profile, ability to grow on waste substrates and demonstrated success as aquaculture feed. However, to support the wide-scale application of PNSB SCP, concerns such as negative opinions associated with non-traditional food sources, improving biomass yield and reducing the cost of extraction processes will need to be addressed.

Fine Chemical Production

Carotenoids are lipophilic pigments produced by bacteria, plants, algae, yeast, and filamentous fungi. They absorb light in the 400–550 nm range, which gives them their characteristic red, yellow, and orange colors and earns them their role in both photosynthesis and phytoprotection (Armstrong & Hearst, 1996). All carotenoids are composed of eight isoprenoid units and can be classified based on whether there is oxygen in one or more functional side groups (xanthophylls) or not (carotenes). These compounds are widely used in food, cosmetics, and pharmaceuticals, and although they can be readily chemically synthesized, even low concentrations of synthetic carotenoids are toxic (Irwandi Jaswir, 2011). Microorganisms offer a safer alternative with the convenience of flexible growth conditions and modularity in color selection, amount, and optional properties of the carotenoids produced (Sundararajan & Ramasamy, 2024). Generally, eukaryotes and archaea use the mevalonate pathway to generate the isoprene precursors for carotenoid production, while bacteria use the methylerythritol pathway (MEP) (Ye & Bhatia, 2012). Both pathways are used to generate 5-carbon isopentenyl pyrophosphate and dimethylallyl diphosphate, which can in turn be synthesized and elongated from 10C geranyl pyrophosphate to 40C phytoene before conversion to lycopene. From here, a series of cyclases, hydroxylases, and ketolases can be used to modify the base structure and give different colors and interactive properties (Sundararajan & Ramasamy, 2024).

As photosynthetic organisms, PNSB naturally produce large amounts of concentrated carotenoids in their photosynthetic compartments. Several groups have determined the genetic pathways required to produce carotenoids of interest, specifically the *crt* cluster, which encodes enzymes to perform functions like phytoene desaturation (CrtI), C-3,4 desaturation (CrtE), C-1,2 hydration (CrtC), and more (Takaichi, 2009; Wang et al., 2012). In PNSB, the two main pathways for carotenoid production are the spirilloxanthin and okenone pathways, although many species have been observed to make unusual compounds outside these pathways, including carotenoid sulfates, glucosides, and acids (Takaichi, 2009). Several groups have achieved notable carotenoid production in a variety of PNSB: Soon *et al.* measured carotenoid production of >0.75 mg/gDCW using PNSB *Afifella marina* isolated from a mangrove habitat (Soon et al., 2014). In a less natural habitat, Saejung & Ampornpat reached 7.2 mg/gDCW with *R. faecalis* PA2, which was isolated from a domestic wastewater treatment pond (Saejung & Ampornpat, 2019). Yu *et al.* optimized light source conditions for *R. sphaeroides* photoheterotrophic growth and under infrared light achieved total carotenoid levels of 22 mg/L (Yu et al., 2021). Infrared light is frequently used to keep PNSB cultures pure as they are exceptionally skilled at capturing this wavelength. This group also demonstrated that incandescent light resulted in the highest protein content, which could prove useful for SCP applications. Genetic engineering has also been employed to improve specific carotenoid content by routing precursors away from competing pathways: Wang *et al.* achieved high levels of lycopene production by deleting *crtC* and *crtD* in *R. rubrum*, effectively preventing the conversion of lycopene to downstream carotenoids such as spirilloxanthin (Wang et al., 2012).

Since carotenoid production is directly tied to photosynthesis, this technology faces the familiar issue of requiring high light-efficiency reactor setups to encourage maximum production. However, a balance must be maintained between the photoinhibitory effects of prolonged high light intensity and the tendency of cells to degrade unused photosynthetic machinery in darkness. Intensity and photoperiod (light/dark cycle) have pronounced effects on the level and type of carotenoid production as well. Liu *et al* saw that *R. palustris* produced the highest amounts of carotenoids (~2 mg/g biomass) and bacteriochlorophyll (~1.2 mg/g biomass) at 150 μmol-photons/m^2/s with a light/dark cycle of 16 h/8 h, respectively (Liu et al., 2019). Alternatively, using a different strain of *R. palustris* Lopez-Romero *et al.* observed up to 8.8 mg/g biomass with 30 μmol-photons/m^2/s under continuous illumination supplemented with nitrogen and carbon sources (Lopez-Romero et al., 2020). In short, optimization of light availability will be dependent on the strain, substrate and reactor design. Another major issue is the extraction and purification of carotenoids, which constitutes a large portion of production costs. Since carotenoid structures vary in polarity and defining molecular traits, there is no single solvent or method that will

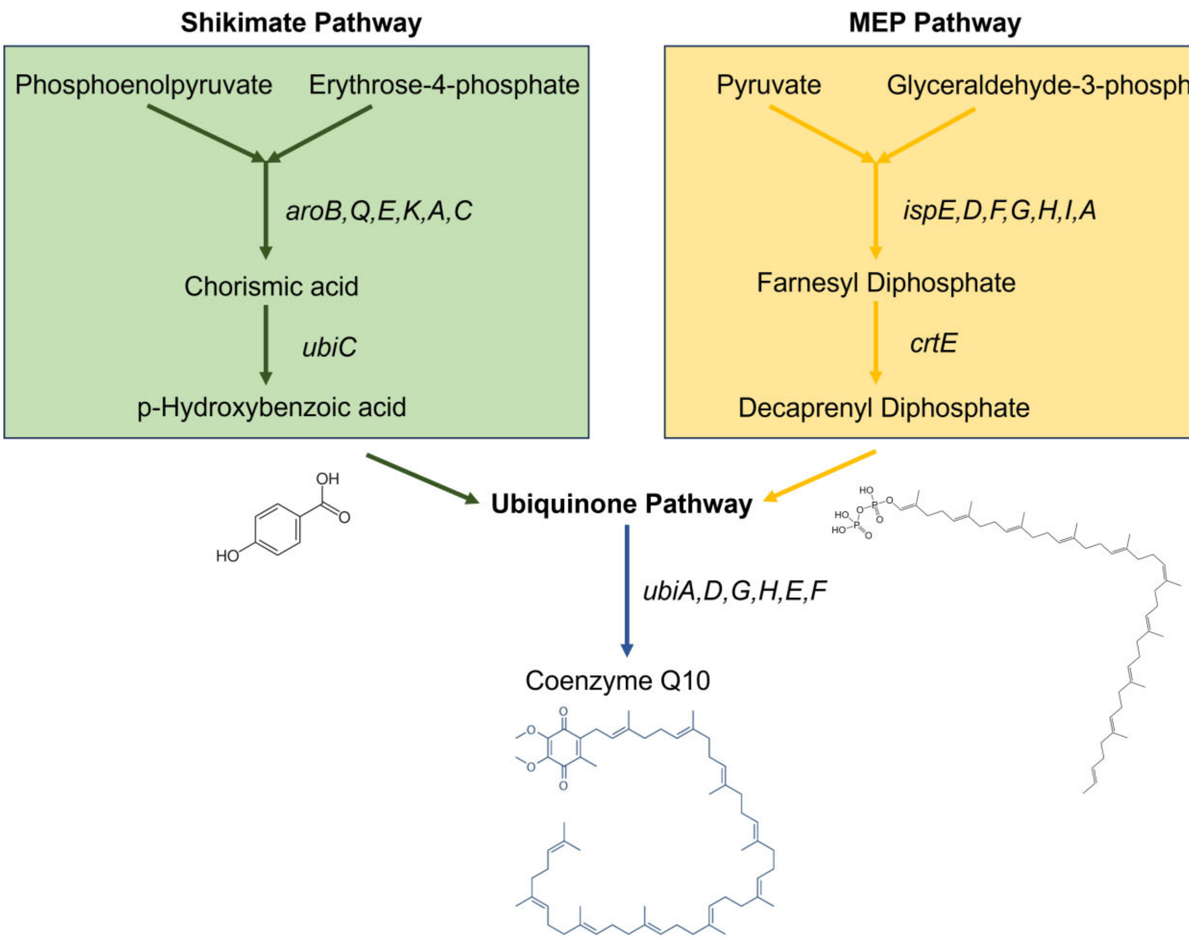

Fig. 3. Simplified metabolic pathways for Coenzyme Q10 production in PNSB. The shikimate pathway (left) is used to produce the quinone core, *p*-hydroxybenzoic acid, to be synthesized with long chain fatty acid decaprenyl diphosphate from the methylerythritol 4-phosphate (MEP) pathway (right) via the ubiquinone pathway to produce Coenzyme Q10 (bottom). Italicized gene names indicate the cluster utilized for that production step.

work across the board. Broadly, carotenes require non-polar solvents and xanthophylls require polar, however the extraction process also involves steps to disrupt the cell wall and characterize the recovered compounds. For a more complete review of these techniques, readers are directed to López *et al* (2023).

Coenzyme Q10 (CoQ10) is a member of the ubiquinone family, which are 5,6-dimethoxytoluquinones with varying length polyisoprenoid side chains at the 6-position of benzene. They contribute to ATP production by serving as electron carriers in the ETC and are strong antioxidants. CoQ10 is frequently used to protect fat-containing products–such as cosmetics and pharmaceutical products–from oxidation and has proven therapeutical benefits for cardiomyopathy and muscular dystrophy (Sasikala & Ramana, 1995; Shukla & Dubey, 2018). Its purported health benefits have led to an increased commercial demand for CoQ10, and while it can be artificially synthesized or extracted, extraction yields tend to be far lower than microbial production (4–2000x lower) and chemical synthesis requires expensive catalysts (He et al., 2021). Photosynthetic microbes often have higher production levels than non-photosynthetic, and PNSB even more so. PNSB can naturally produce up to 80 mg/L, with most strains performing best under photohetero- or mixotrophic modes (He et al., 2021). *R. sphaeroides* is considered to be the best producer of CoQ10 and is often the focus of efforts to optimize production. Zou *et et* used a modified mutagenizing treatment to obtain *R. sphaeroides* AR01, which could produce ∼330 mg/L CoQ10, a nearly 25% increase in production from the parent strain (Zou et al., 2019). Alternatively, Zhang *et al* used a more targeted approach by deleting genes encoding the catalytic subunits of key enzymes related to the ETC in *R. sphaeroides* 2.4.1. They found that the deletion of succinate dehydrogenase, responsible for transferring electrons from succinic acid to CoQ10, combined with a variable aeration scheme could increase production up to 40% compared to wildtype (Zhang et al., 2018). The pathway used to produce CoQ10 is shown in Fig. 3, where the shikimate pathway is used to produce the quinone core and the MEP pathway produces the isoprenoid side chain. Given that carotenoid synthesis also uses MEP to produce lycopene, this puts CoQ10 production in direct competition for resources. Thus, the organism is typically optimized to produce one or the other. PNSB CoQ10 production has been optimized both genetically (e.g. modifying regulators, deleting competing enzymes) and by altering environmental conditions (e.g. light source, carbon source, reactor type) for multiple species, but much work remains to implement this on a broader commercial scale (For a full review, readers are directed to He *et al.* 2021). Similar to carotenoid production, extraction of CoQ10 also represents a significant portion of production cost and currently employs harmful organic solvents (Wu & Tsai, 2013). Despite lab-scale success with methods like column chromatography, such methods remain too expensive for commercial application (Deng et al., 2019). Cost can also be reduced

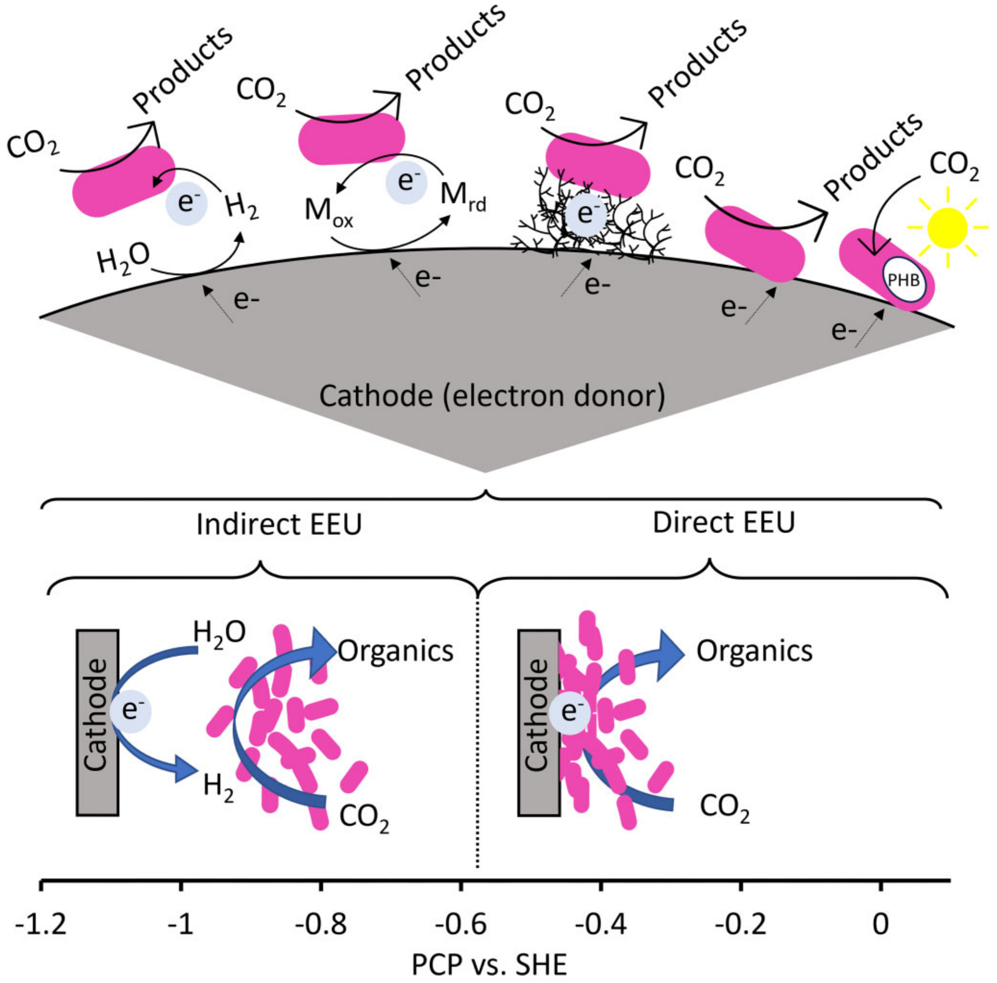

Fig. 4. Mechanisms of extracellular electron uptake (EEU) from a cathode in PNSB. (Top) PNSB fix CO_2 to form bioproducts using electrons from (left to right) indirect uptake using H_2 produced from water hydrolysis, indirect uptake using reduced metals or other redox carriers, direct uptake using a conductive material matrix, and direct uptake via cell surface-to-electrode surface contact. (Top, far right) An example of photoautotrophic generation of poly-hydroxybutyrate (PHB) using electrons from the cathode. (Bottom) For *R. palustris* TIE-1 at potentials below −0.6 V, indirect EEU is favored to occur via hydrolyzed H_2; above −0.6 V direct attachment to the cathode is observed. Adapted with permission from Karthikeyan *et al.* 2019.

by using non-toxic waste inputs, as with other technologies, and coupling production to wastewater treatment, but this has yet to be implemented at an industrial scale.

Avant-Garde Technologies

Aside from the traditional biotechnology applications discussed above, PNSB must also be considered for their unique metabolic capabilities: for example, exchanging electrons between solid phase conductive substances including minerals and poised electrodes.

Electroactive microorganisms are identified by their ability to perform EET. They are classified as either electrotrophs (capable of consuming electrons from extracellular sources such as reduced minerals or cathodes), or exoelectrogens (capable of releasing electrons to external electron acceptors such as oxidized minerals or anodes). Some electroactive microbes engage in bi-directional electron transfer. These organisms play critical roles in biogeochemical cycling and as members of a wide range of microbiomes, including extremophilic environments, intestinal systems, and anaerobic soils (Lovley & Holmes, 2022). There are several methods of EET utilized by different species that can be broadly separated into direct and indirect strategies. As depicted in Fig. 4, direct strategies involve direct contact between the microbe and the conductive surface, such as via protein nanowires or the extracellular matrix, while indirect strategies favor the use of electron shuttles like quinones and H_2. The exact strategy used depends on the strain and environmental conditions, but several gene clusters have been identified to assist in predicting the electro-strategies available to an organism. For example, there is substantial evidence that porin-cytochrome complexes are involved in electron transport to the outer cell surface in gram-negative organisms; the presence of multi-heme *c*-type cytochromes in metagenomes has been used to successfully predict EET involvement (Arbour et al., 2020). In PNSB, *R. palustris* TIE-1 is identified to be capable of extracellular electron uptake (EEU) via the *pio ABC* operon; specifically, that PioA (decaheme cytochrome *c*) and PioB (outer membrane porin) form a complex to allow EEU across the outer membrane. Although originally studied under photoferrotrophic conditions, EEU can occur via a cathode as well (Bose et al., 2014; Gupta et al., 2019).

Substantial interest in exploring the capabilities of electroactive organisms has recently developed as the global community searches for sustainable methods of production and bioremediation. One such method is *microbial electrosynthesis,* which refers to the use of electrons from a biocathode to produce valuable compounds, including PHA, hydrogen gas, and more (Manchon, Muniesa-Merino, et al., 2023a). PNSB are once again favored here for their ability to use renewable and cheap inputs and create a broad range of valuable products. For example, as discussed in section Wastewater Treatment, one of the ways to reduce the cost of the application is to recover resources from wastewater, which PNSB is highly skilled at. Manchon *et al.* not only found that a *Rhodopseudomonas*-dominated non-sterile PPB mixed culture could grow photo-autotrophically with a cathode as the sole electron donor (−0.6 V vs. Ag/AgCl) (Manchon et al., 2023b) but further demonstrated the enhancement of PPB biomass when grown in a fluid-like electrode on brewery wastewater (−0.6 V vs. Ag/AgCl) compared to an electrode-free control (Manchon et al., 2023a). This phenomenon of an additional source of electrons supporting higher biomass production was also observed by Guzman *et al.* who found that the majority of electrons consumed by *R. palustris* during cathodic photoautotrophic growth are used for carbon fixation and ensuing biomass production (Guzman et al., 2019). Intriguingly, this carbon fixation even occurs under photoheterotrophic conditions from −0.2 to −0.8 V, although the authors note that other electron sinks beside the CBB are likely in play (Edreira et al., 2021). Further study of these electron sinks may help direct genetic engineering efforts to further increase biomass production by limiting electron flow to extraneous pathways. PNSB production of conventional bioproducts via electrotrophy can also be achieved; Ranaivoarisoa *et al.* found that *R. palustris* TIE-1 produced PHB when grown autotrophically on either a poised cathode or reduced iron (Ranaivoarisoa et al., 2019). Rengasamy *et al.* took this a step further by using a modified cathode (magnetite nanoparticles and reduced graphene oxide nanocomposite) to improve PHB production by more than four times compared to electrotrophic growth with an unmodified carbon felt cathode (Rengasamy et al., 2020). Alternatively, as discussed in section Biofuels, H_2 production can also be achieved via cathode, although this study supplemented growth with organic acids (Vasiliadou et al., 2018). Although microbial electrosynthesis with PNSB has only recently begun to be seriously explored, these phototrophs demonstrate the potential to achieve biotechnologically relevant outcomes—with plenty of optimization.

An alternative application would be the co-culture of PNSB with a partner that either feeds PNSB with metabolites or benefits from the by-products produced by PNSB. Co-culture can reduce the individual metabolic burden on a single species while still allowing for the production of specialized products and/or utilization of renewable inputs. By co-cultivating aerobic heterotrophs (AH) with PNSB, which are both respectable SCP sources alone, in a sequential photo- and chemotrophic approach Alloul *et al.* improved protein content by >45% and produced a more attractive amino/fatty acid profile compared to AH alone (Alloul et al., 2021b). This method also resulted in a 30% lower production cost compared to separate cultivation, largely owing to a reduced volume of the photobioreactor used to grow PNSB. Also in the vein of improving SCP, Adcock showed that *Rubrivivax gelatinosus* could achieve significant growth using the byproducts of methanotroph *Methylosinus sporium* growing on CH_4 as the sole carbon source (Adcock, 2022). Alternatively, PNSB growth can be improved by the partner altering environmental conditions; Arashida *et al.* found that *R. palustris,* which cannot fix nitrogen in the presence of oxygen, was able to fix N_2 at ∼21 vol.% oxygen when grown with *Bacillus subtilis* which consumes oxygen (Arashida et al., 2019). Looking at sustainable inputs, Lu & Lee co-cultivated *R. palustris* CGA009 with *Clostridium cellulovorans* 743B on cellulose as the sole carbon source, and found that cellulose degradation and hydrogen production increased compared to the monocultures (Lu & Lee, 2015). Despite these successes, it should be kept in mind that co-culture between two or more species is often a double-edged approach; while it can allow for the consumption of cheaper resources or more easily complete a process (i.e. wastewater treatment with a consortium), the user loses fine control over the community, and it becomes more difficult to predict response to change. Thus, even with two species, it is worthwhile to thoroughly consider their metabolic interactions in order to predict broader responses to environmental changes.

Future applications might look to combine the electron-exchanging abilities of PNSB and their potential for co-culture by exploring growth using a bio-electrode setup. By capitalizing on the use of renewable carbon sources and, depending on the reactor, renewable energy sources (i.e. solar power) it may be possible to improve sustainability and product output while reducing production costs.

Conclusion

In this review, we discussed the metabolic capabilities of PNSB and how they are leveraged for biotechnological applications. Their unique metabolism offers advantages for use in energy production, wastewater treatment, and resource recovery, as well as fertilizer production and SCP. They are also capable of fine chemical production (e.g. carotenoids and CoQ10), and have begun to be explored in depth for their ability to perform electrotrophy and promote valuable compound production in co-culture. The ability of PNSB to use a variety of electron donors and grow under a wide range of environmental conditions make them a suitable candidate for overcoming the high industrial cost points of feedstock and culturing conditions. Many groups have already demonstrated their ability to grow on and remediate wastewater, and optimization of reactor conditions continues to develop beyond lab-scale. In the future, PNSB will undoubtedly play a critical role in developing the CE in the global shift towards a sustainable way of life.

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Conflict of Interest

The authors declare no conflict of interest.

Data Availability

No new data were generated or analyzed in support of this research.

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