Biotechnology Advances 60 (2022) 108001

Contents lists available at ScienceDirect

Biotechnology Advances

journal homepage: www.elsevier.com/locate/biotechadv

Research review paper

Rhodopseudomonas palustris: A biotechnology chassis

Brandi Brown [a], Mark Wilkins [a,b,c], Rajib Saha [d,*]

[a] Department of Biological Systems Engineering, University of Nebraska-Lincoln, Lincoln, NE 68583, USA
[b] Industrial Agricultural Products Center, University of Nebraska-Lincoln, Lincoln, NE 68583, USA
[c] Department of Food Science and Technology, University of Nebraska-Lincoln, Lincoln, NE 68588, USA
[d] Department of Chemical and Biomolecular Engineering, University of Nebraska-Lincoln, Lincoln, NE 68588, USA

ARTICLE INFO

Keywords:
Rhodopseudomonas palustris
Cell factory
Bioprocessing
Industrial biotechnology
Purple non-sulfur bacteria
Bioremediation
Biostimulant
Hydrogen
Electricity
Bioplastic

ABSTRACT

Rhodopseudomonas palustris is an attractive option for biotechnical applications and industrial engineering due to its metabolic versatility and its ability to catabolize a wide variety of feedstocks and convert them to several high-value products. Given its adaptable metabolism, *R. palustris* has been studied and applied in an extensive variety of applications such as examining metabolic tradeoffs for environmental perturbations, biodegradation of aromatic compounds, environmental remediation, biofuel production, agricultural biostimulation, and bioelectricity production. This review provides a holistic summary of the commercial applications for *R. palustris* as a biotechnology chassis and suggests future perspectives for research and engineering.

1. Introduction

Rhodopseudomonas palustris is a metabolically robust bacterium that can catabolize a wide variety of feedstocks and turn them into several high-value products, making it an attractive option for biotechnical applications and industrial engineering. This Gram-negative purple non-sulfur bacterium is renowned for its ability to function in the four known metabolisms of life (Larimer et al., 2004). Under lighted conditions, *R. palustris* can use energy from light and obtain carbon from carbon dioxide (photoautotrophic or photosynthetic) or obtain carbon from organic compounds (photoheterotrophic). Alternatively, it can obtain carbon and energy from organic compounds (chemoheterotrophic) or garner energy from inorganic compounds (e.g. thiosulfate) while obtaining carbon from carbon dioxide (chemoautotrophic). *R. palustris* is renowned for its exceptional ability to flexibly switch between these modes of metabolism depending on the environmental conditions. It is commonly found in a wide variety of environments, and has been isolated from sources such as sludge, soils, aquatic sediments, alkaline waters, rice straw, leaf litters, and eutrophic ponds (Rayyan et al., 2018). *R. palustris* was first identified by van Niel in 1944, and the first genome sequence of strain CGA009 was determined in 2004 (Larimer et al., 2004). This was followed by the complete genome sequence of strain JSC-3b in 2014, which is known for degrading pyrethroid pesticides (Zhang et al., 2014). The essential genome of strain CGA009 was determined in 2015 and provides a detailed synopsis of the genes that are absolutely necessary for viability (Pechter et al., 2015). Strain 420 L has been extensively employed for biohydrogen production and even for novel antibiotic delivery via its liposomes (Colzi et al., 2015), and the draft genome sequence was accomplished in 2016 (Adessi et al., 2016a). The complete genome sequence of strain ELI 1980 was obtained in 2017, and this strain has been applied as a commercial agricultural biostimulant (Crovadore et al., 2017). In 2018, the draft whole-genome sequence for strain XCP was accomplished, which was identified as a new strain based on variations in cytochrome c_2 compared to other strains (Rayyan et al., 2018). However, there have been many other strains isolated across the globe that have been applied in a variety of biotechnical applications that have yet to be sequenced (Table 1). Due to its versatile metabolism, *R. palustris* has been studied and applied in a wide variety of applications such as biodegradation of aromatic compounds, environmental remediation, biofuel production, agricultural

---

Abbreviations: BPVs, Biophotovoltaics; CBB, Calvin-Benson-Bassham; MERS, Microbial electrochemical remediation systems; MFCs, Microbial fuel cells; PHBV, Poly-3-hydroxybutyrate-*co*-hydroxyvalerate; PHB, Poly-β-hydroxybutyrate; PHAs, Polyhydroxyalkonoates; PLA, Poly(lactic) acid; Rubisco, Ribulose-1,5-bisphosphate carboxylase/oxygenase.

* Corresponding author.

E-mail address: rsaha2@unl.edu (R. Saha).

https://doi.org/10.1016/j.biotechadv.2022.108001
Received 25 January 2022; Received in revised form 18 May 2022; Accepted 1 June 2022

Table 1
Highlighted *R. palustris* strains and their applications.

Application	Strain	Remarks and References
Genome sequence available	CGA009	(Larimer et al., 2004; Pechter et al., 2015)
	JSC-3b	(Zhang et al., 2014)
	42OL	(Adessi et al., 2016a)
	ELI 1980	(Crovadore et al., 2017)
	XCP	(Rayyan et al., 2018)
Biohydrogen production	CGA009	(Alsiyabi et al., 2021, 2019; Egland et al., 2001; Gosse et al., 2010; Oshlag et al., 2020)
	42OL	(Adessi et al., 2012; Corneli et al., 2017)
	CQK 01	(Liao et al., 2013; Tian et al., 2010, 2009; Wang et al., 2013, 2012)
	DSM 127	(Azbar and Cetinkaya Dokgoz, 2010)
	DSM 131	(Fiβler et al., 1995)
	ATH2.1.37	Heat-acclimated overproduction (du Toit and Pott, 2021)
	JA1	(Archana et al., 2003)
	P4	H_2 production from syngas (carbon monoxide) (Hosseini et al., 2015; Oh et al., 2005)
	PBUM001	(Jamil et al., 2009)
	WP3–5	Deleted bioplastic genes to promote more biohydrogen production (Yang and Lee, 2011)
Bioelectricity production	TIE-1	(Bai et al., 2021; Guzman et al., 2019; Rengasamy et al., 2018)
	Azul	(Guardia et al., 2020)
	DX-1	(Rengasamy et al., 2020; Xing et al., 2008)
	CGA009	(Morishima et al., 2007; Qi et al., 2018b)
	RP2	(Venkidusamy and Megharaj, 2016)
	PS3	(Hsu et al., 2021; Liu et al., 2021; Lo et al., 2020; Wong et al., 2014)
Bioplastic production	CGA009	(Alsiyabi et al., 2021; Brown et al., 2020, 2022; Tian et al., 2017)
	TIE-1	(Ranaivoarisoa et al., 2019; Rengasamy et al., 2020)
Agricultural production	CS2	Biostimulant for beans (*Vigna mungo*) (Batool et al., 2017)
	GJ-22	Biostimulant (resistance to tobacco mosaic virus) (Su et al., 2017)
	P1	Biostimulant for rice (Kantha et al., 2015)
	PP803	Biostimulant for rice (Kantachote et al., 2016; Kantha et al., 2015)
	PS3	Biostimulant for Chinese cabbage (Hsu et al., 2021; Lo et al., 2020; Wong et al., 2014)
	TK103	Biostimulant for rice (Kantachote et al., 2016; Kantha et al., 2015)
Biodegradation	CGA009	Extensively studied for aromatic compound degradation; cleaning waste waters of organics and heavy metals; consuming chemicals used in fuel processing; remediation of farm chemicals (e.g. pesticides); catabolism of lignocellulosic biomass (Alsiyabi et al., 2021; Brown et al., 2022; Colica et al., 2012; Austin et al., 2015; Egland et al., 2001; Gao et al., 2017; Gosse et al., 2010; Harwood and Gibson, 1988; Hidetada et al., 2012a; Berne et al., 2005, 2007; Ma et al., 2021; Mutharasaiah et al., 2012; Oshlag et al., 2020; Rahalkar et al., 1993)
	PSB07–21	Biodegradation of pesticides (Luo et al., 2018)
	PSB-S	Biodegradation of pesticides (Luo et al., 2018)
	WS17	Dechlorination (Kamal and Wyndham, 1990)
	WKU-KDNS3	Skatole degradation from animal wastes (Sharma et al., 2015)
	YSC3	Biodegradation of hexabromocyclododecane (Chang et al., 2020; Wang et al., 2019a)
	AS1.2352	Azo dyes decolorization (Liu et al., 2006)
	GJ-22	Biodegradation of cypermethrin pesticides (Su et al., 2017)
	JSC-3b	Pyrethroid degradation (Zhang et al., 2014)
	RCB-100	Degradation of 3-chlorobenzoate (Haq and Fixen, 2021)
	RSOU555	Removal of organics from waste waters (Bogarapu et al., 2019)
	P1	Nitrogen removal from aquaculture wastewater (Xiao et al., 2020)
	PSB-1D	Optimized o-chlorophenol degradation (Dong et al., 2017)

biostimulation, and electricity production (Fig. 1). This review provides a holistic summary of the commercial applications for *R. palustris*, as well as future perspectives.

2. *R. palustris* as a model organism for flexible metabolism

R. palustris has emerged as a model organism for understanding how microbes respond to environmental perturbations at a systems level. *R. palustris* has exceptional flexibility to switch between the four modes of metabolism that support life, rendering it an ideal candidate for developing a deeper fundamental understanding of how organisms adapt to their environments (Larimer et al., 2004). Known to straddle oxic and anoxic transition zones, *R. palustris* can flexibly switch between aerobic respiration under atmospheric levels of oxygen to photosynthesis under anaerobic or oxygen depleted conditions (2–6% O_2) (Fig. 2). *R. palustris* oxidizes carbon compounds for carbon and energy when exposed to atmospheric levels of oxygen via aerobic respiration, and when exposed to anaerobic or oxygen depleted conditions it begins to generate light absorbing pigments necessary for photosynthesis that render it the deep purple color it is known for (Harwood, 2022; McKinlay et al., 2014; Rey and Harwood, 2010).

R. palustris has emerged as model bacterium for understanding photosynthesis because it can perform anoxygenic photosynthesis, employing cyclic photophosphorylation without generating oxygen (Rey and Harwood, 2010). It has also served as a model organism for adaptations to changing light conditions since it engages phytochromes that alter gene expression, providing insight into various strategies for responding to solar energy and optimizing photon capture (Evans et al., 2009). Under low levels of oxygen, *R. palustris* conducts nitrogen fixation and can use atmospheric nitrogen as its sole nitrogen source (Rey and Harwood, 2010). As a byproduct of nitrogen fixation, *R. palustris* produces hydrogen and ammonium and has thus been extensively studied for biohydrogen fuel production. *R. palustris* employs two forms of the enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), which is responsible for the majority of biologically fixed CO_2 on Earth. There has been significant effort to engineer Rubisco since it is a relatively inefficient biocatalyst for the critical reaction in the Calvin-Benson-Bassham (CBB) reductive pentose phosphate pathway (Rey and Harwood, 2010). *R. palustris* has served as a means to better understand this reaction mechanism and for deciphering differences in the forms of Rubisco enzymes (Satagopan et al., 2014). Due to *R. palustris'* ability to adapt to a wide variety of environments, it has also served as a platform for investigating biofilm formation under various conditions since the impact of biofilm formation during various metabolic growth modes can be investigated in a single species (Kernan et al., 2015). Findings, such as a novel quorum sensing synthase employed by *R. palustris* that is not tied to fatty acid metabolism (Schaefer et al., 2008), have expanded our understanding of biofilm formation in other organisms as well. Being able to either limit or encourage biofilm formation is key to optimized

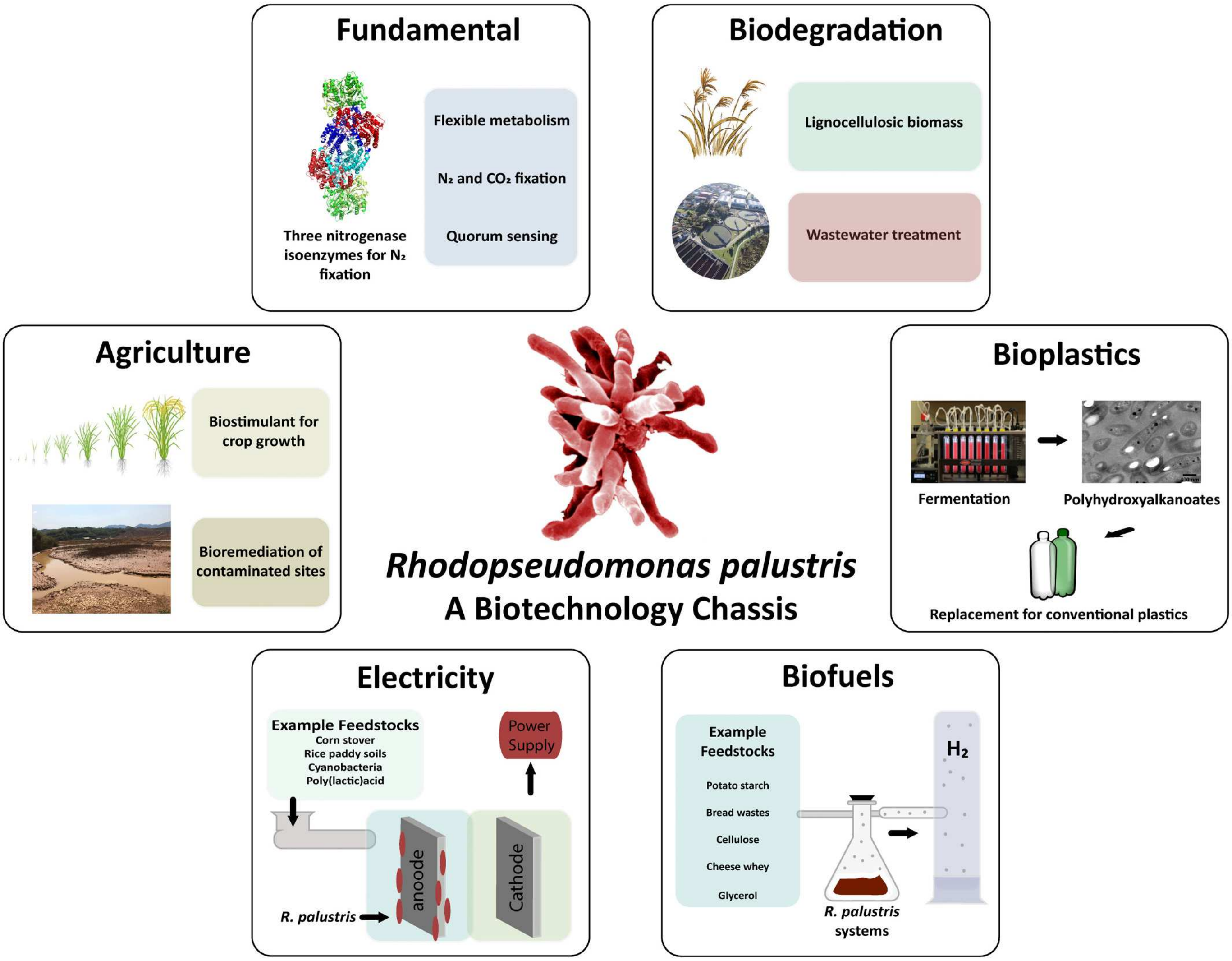

Fig. 1. *R. palustris* as a biotechnology chassis. *R. palustris* is a metabolically diverse purple non-sulfur bacterium and a developing biotechnology chassis. *R. palustris* has been applied in many applications such as developing a deeper fundamental understanding of tradeoffs between metabolisms, biodegradation, biofuels, bioplastics, electricity systems, and agricultural production.

engineering for many applications in the biomedical and bioprocess engineering industries. Lastly, 15% of *R. palustris'* genome consists of genes that encode for transport systems, which is triple that found in most bacterial genomes (Bisson et al., 2022; Larimer et al., 2004; Pechter et al., 2015). *R. palustris* has therefore been studied extensively for the transport and degradation of a wide variety of compounds (please see Section 3).

The "omics" revolution combined with advances in metabolic modeling have provided a platform for understanding *R. palustris* at a systems level. Newer genome-scale metabolic modeling techniques enable simultaneous comparisons of biological trade-offs from several objectives and constraints. A recent metabolic model identified that phototrophic metabolism in *R. palustris* is limited by light and not by the availability of carbon, and that *R. palustris* will still strive for maximum carbon efficiency even if this efficiency results in lower growth rates (Navid et al., 2019). A genome-scale metabolic model was also employed to decipher tradeoffs and connections between photosynthesis, CO_2 fixation, and the quinone pool by *R. palustris* (Alsiyabi et al., 2019). This model identified several key factors for employing excess electrons produced during metabolic processes that can be further exploited. These findings included identifying a quinol-oxidizing sink reaction that had not been accounted for previously, that the quinol oxidation rate governs light-dependent energy production, and the amount of ATP generated in the electron transport chain directly impacts the extent of CO_2 fixation (Alsiyabi et al., 2019). A recent metabolic expression model builds upon this knowledge to further explore the interconnectedness of Rubisco and nitrogenase enzymes in anaerobic-photoheterotrophic conditions, predicting two more electron sinks and identifying ferredoxin as a modulator of electron flux through major redox pathways in the cell (Chowdhury et al., 2022).

In summary, *R. palustris* is an excellent candidate for studying the systems-level metabolic tradeoffs between major forms of metabolism. As more information is available that can feed into increasingly sophisticated genetic engineering and metabolic modeling, such as the availability of metabolic flux analysis models, deeper understanding about tradeoffs between modes of metabolism can be found from a systems perspective.

3. The use of *R. palustris* in biodegradation applications

The biodegradation of aromatic compounds has received much attention due to their persistence, toxicity, and renewability. *R. palustris* is renowned for its ability to catabolize a wide variety of aromatic compounds, which makes it an excellent candidate for applications in bioremediation and utilizing renewable aromatics like those from lignocellulosic biomass. The biochemical pathways for anaerobic

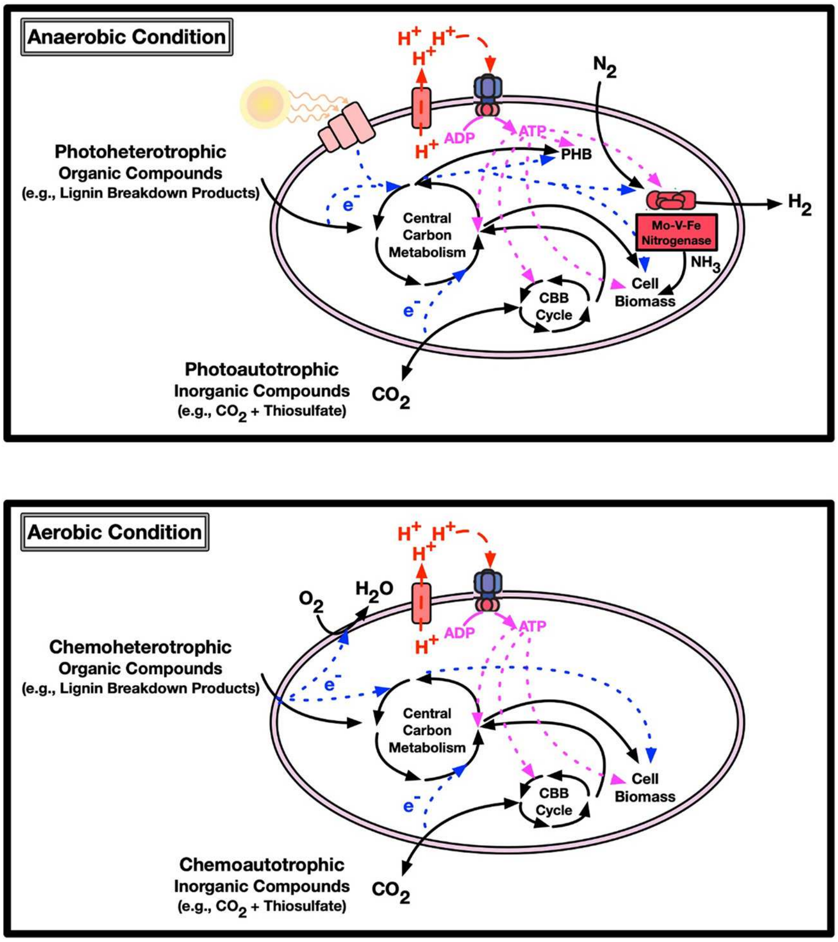

Fig. 2. The major metabolic core states that *R. palustris* is renowned for flexibly switching between. Under anaerobic conditions, *R. palustris* generates ATP through cyclic phosphorylation from light whereby electrons are cycled through a proton-pumping electron transport chain rather than using a terminal electron acceptor. It can use either organic compounds (photoheterotrophic) or inorganic compounds and CO_2 (photoautotrophic). Note that there are tradeoffs in utilizing reducing potential between biomass production, polyhydroxyalkanoate formation, and nitrogen fixation. Under aerobic conditions without light, *R. palustris* employs proton motive force to transfer electrons to a terminal electron acceptor (e.g. O_2, dimethyl sulfoxide, potassium nitrate, or sodium nitrite) to produce a hydrogen gradient and ultimately generate ATP for energy. In this case, *R. palustris* uses either organic compounds (chemoheterotrophy) or inorganic electrons donors and CO_2 (chemoautotrophy) under aerobic conditions.

benzoate and 4-hydroxybenzoate degradation have been characterized extensively, illuminating novel steps in the biodegradation pathway (Egland et al., 1995; Hirakawa et al., 2015). For example, AadR and HbaR are members of the fumarate and nitrate reductase (FNR) family of transcriptional regulators that foster a cascade system in *R. palustris* that activates expression of genes sensing 4-hydroxybenzoate, fosters transcription of degradation genes, and thereby triggers biodegradation of the aromatic pollutants (Díaz and Prieto, 2000). Thus, specific regulator-promoter pairs have been identified in *R. palustris* for the catabolism of aromatic compounds that can be expanded upon for engineering more efficient systems in the future.

Hydrocarbon contamination is found in environments worldwide, and microbial degradation has become a promising strategy for remediation and recovery. Petroleum is the base material for many of today's products from plastics to cosmetics, and *R. palustris* has been applied to mitigate aromatic hydrocarbon contamination through petroleum removal in marine environments via the transformation of toluene to benzoyl-CoA (Harayama et al., 1999; Rhee et al., 2004), flame retardants (Chang et al., 2020; Li et al., 2021; Wang et al., 2019a), and polycyclic aromatic hydrocarbon degradation (Zhao et al., 2011). *R. palustris* is also capable of degrading polyesters such as the bioplastic poly(lactic) acid (PLA), which is considered a potential replacement for conventional plastics (Hajighasemi et al., 2016; Qi et al., 2017; Wang et al., 2019c). Thus, *R. palustris* shows promise as a robust chassis for the remediation of both aromatic and non-aromatic hydrocarbon contaminants.

As a photosynthetic bacterium with high tolerance and flexible metabolic modes, *R. palustris* has also been employed for wastewater remediation. Sustainable wastewater treatment has reached a paradigm shift from removing unwanted pollutants to salvaging resources and producing energy. Alternative methods to replace conventional activated sludge methods are arising to develop more sustainable protocols and combat some of the leading challenges associated with wastewater treatment (e.g. nutrient recovery and degradation efficiency). The feasibility of utilizing photosynthetic bacteria for wastewater treatment has been extensively studied since they can be used to deliver more complete nutrient capture in wastewater, absorb CO_2, deliver diversification of products, and their biomass can be recycled for downstream processing (Chen et al., 2020b). A recent review provides an overview of photosynthetic-based technology for wastewater treatment and details the photosynthetic membrane bioreactor systems in which *R. palustris* has been applied (Chen et al., 2020b). *R. palustris* has been specifically studied for removal of heavy metals from wastewater (Gao et al., 2017), biosorption and recovery of ruthenium from industrial effluents (Colica et al., 2012), consumption of oils (Padovani et al., 2018; Phongjarus et al., 2018), decolorization and mineralization of dyes (Çelik et al., 2012; Liu et al., 2006; Wang et al., 2008), processing farm chemicals and wastewaters (Dong et al., 2017; Kim et al., 2004; Mutharasaiah et al., 2012; Phongjarus et al., 2018; Wu et al., 2019), salinity tolerance (Qin et al., 2017), efficient culture using landfill leachate (Wang et al., 2018), dichlorination (Egland et al., 2001; Kamal and Wyndham, 1990), and the degradation of chemicals used in fuel processing (Berne et al., 2007, 2005).

R. palustris is also a promising biotechnology chassis for the production of high value products from the biodegradation of lignocellulosic biomass. With an estimated annual production of over 200 billion tons, lignocellulosic biomass from plants is a common agricultural waste and highly renewable carbon source with relatively high economic potential compared to other renewable feedstocks (Ponnusamy et al., 2019; Qian, 2013). Lignin comprises a large portion of lignocellulosic biomass and is the most abundant aromatic polymer on Earth, with the potential to replace fossil fuels as a source of renewable aromatic compounds (Lee et al., 2019). Unfortunately, many microbes are unable to catabolize it and are often inhibited by it due to its toxicity and inhibition of enzymes (Lee et al., 2019). The production of biopolymers from lignin has emerged as one of the most promising routes for valorizing lignin, and thus engineering a microbe that can catabolize it for high-value products is ideal (Banu et al., 2019). As a metabolically robust bacterium, *R. palustris*' genome includes pathways for aerobic and anaerobic pathways for three of the four known microbial lignin degradation strategies, including the 3,4-dihydroxyphenylacetate, *p*-coumarate, and phenylacetate catabolic pathways (Bisson et al., 2022; Elder et al., 1992; Harwood and Gibson, 1988; Larimer et al., 2004; Salmon et al., 2013). Thus, it has the genetic potential for oxygen-sensitive and oxygen-requiring enzyme reaction sequences for complete degradation of lignin aromatics for multiple cell functions like biomass and bioplastic production (Alsiyabi et al., 2021; Harwood and Gibson, 1988; Larimer et al., 2004). Thus far, it has been shown that *R. palustris* can catabolize over two dozen aromatic compounds from lignin (Austin et al., 2015; Harwood and Gibson, 1988). *R. palustris* has emerged as a model organism for anaerobic catabolism of aromatic compounds, particularly for the major lignin breakdown product *p*-coumarate (Doud and Angenent, 2016; Pan et al., 2008; Salmon et al., 2013). Employing *R. palustris* as a means to remove these aromatics so that another microbe may consume sugars or other breakdown products has proved to be a promising strategy for efficiently utilizing pretreated lignocellulosic biomass (Austin et al., 2015). Recent kinetic modeling of anaerobic degradation of lignin aromatics by *R. palustris* highlights the dynamics between the co-metabolism of multiple lignin aromatics and proposes new mechanisms for substrate channeling (Ma et al., 2021). Lastly, although strain CGA009 was shown to be unable to metabolize meta-methoxylated phenolic compounds from lignin, new strains (e.g. SA008.1.07) can be adapted to grow on syringic acid as a sole carbon source (Oshlag et al., 2020).

However, the degradation pathways for many lignin breakdown products remain elusive for *R. palustris*. Furthermore, since *R. palustris* must eliminate excess reducing equivalents during anaerobic degradation of lignin aromatics more effort is needed to develop systems that mitigate lethal redox imbalances through microbial consortia (Doud and Angenent, 2016). Optimizing co-culture systems with *R. palustris* whereby multiple organisms can consume different parts of lignocellulosic biomass could provide for more complete processing into high-value products (Ibrahim et al., 2021; Zhang et al., 2013; Zuroff and Curtis, 2012).

4. *R. palustris* as a biohydrogen powerhouse

There have been attempts to produce biofuels from *R. palustris* such as n-butanol (Bai et al., 2021; Doud et al., 2017), but the majority of research is aimed at biohydrogen production due to *R. palustris'* native capabilities for hydrogen production and its flexibility as a chassis. Hydrogen combustion produces no CO_2 emission, is efficiently converted to electricity when used in fuel cells, and produces an energy yield of 122 kJ/g (about 2.75 times greater than gasoline), making it one of the cleanest possible energy alternatives to fossil fuels (Han et al., 2016; Levin et al., 2004). Biological hydrogen production technologies are considered to be one of the leading options for hydrogen production (Singh et al., 2015). Photo-hydrogen production by photosynthetic bacteria is ranked highest in these promising biological conversion technologies due to the high purity of the hydrogen produced, high theoretical conversion, and the ability to use a variety of feedstocks. *R palustris* has emerged as a model organism for biohydrogen production and has been applied in a wide array of biohydrogen efforts from exploring the biocatalysis mechanisms behind biohydrogen generation to engineering systems to produce sustainable biohydrogen from industrial wastes.

R. palustris is one of very few prokaryotes characterized thus far that encodes three different nitrogenase, the enzyme responsible for converting nitrogen gas into ammonia with the obligatory production of hydrogen. The molybdenum, vanadium, and iron isoenzyme nitrogenases are encoded by the *nif*, *vnf* and *anf* genes respectively (Oda et al., 2005). Thus, *R. palustris* has multiple enzymatic options for nitrogen-fixation and expression of its nitrogenases is not significantly repressed by the presence of transition metals like many other nitrogen-fixing bacteria (Oda et al., 2005). Furthermore, the ability of *R. palustris* to generate H_2 without producing O_2 provides an opportune system for purer hydrogen fuel production. Significantly larger H_2 yields are observed from *R. palustris* when it is starved for nitrogen (e.g. limited nitrogen in the growth media) and cells can utilize the available electrons to synthesize H_2 from nitrogenase (McKinlay et al., 2014). Many synthetic biology efforts have fostered a more fundamental understanding of *R. palustris'* H_2 production abilities under various conditions or created new strains for overproduction. Strains that produce H_2 constitutively even in the presence of ammonium have been selected, and produce up to five times the amount of H_2 compared to the wild-type strain under nitrogen fixing conditions (Rey et al., 2007). The regulatory paradox for why these mutants are able to resist post-translational modifications that would normally inactivate nitrogenases has been illuminated, which revealed that the mutants have insufficient levels of two posttranslational regulation proteins (DraT2 and GlnK2) (Heiniger et al., 2012). A strain containing a variant molybdenum nitrogenase was used to assess tradeoffs in intracellular ADP, light intensity, and gas production that hypothesized that the rate limiting step for H_2 and CH_4 production is inhibition of nitrogenase by ADP. This study revealed several strategies for H_2 and even CH_4 production that included (i) increasing the amounts of electrons available to nitrogenase by providing cells with organic alcohols, (ii) using nongrowing cells, (iii) blocking electrons from entering the Calvin Cycle, and (iv) blocking H_2 uptake (Zheng and Harwood, 2019). Another approach for H_2 overproduction was to delete the bioplastic poly-β-hydroxybutyrate (PHB) synthesis gene *phbC* in *R. palustris* WP3–5 to funnel carbon and reducing potential to H_2 production, which yielded 1.7 times more H_2 than the non-engineered strain (Yang and Lee, 2011). Since oxygen fixation in the Calvin cycle competes with H_2 production for electrons, another study showed that deletion of the upstream phosphoribulokinase (PRK) resulted in both an increase in H_2 yield and specific production rate (McCully and McKinlay, 2016). This provides an alternative strategy to disrupting the Rubisco enzyme, which can cause negative impacts on growth and does not yield an increase in H_2 production rates. New advancements in metabolic modeling also provide avenues for *in silico* investigation of key regulators involved in facilitating redox balance for the cell. A metabolic and expression model was recently created to investigate the interplay of Rubisco and nitrogenase enzymes in anaerobic-photoheterotrophic conditions, which predicted (i) malate dehydrogenase and glycerol-3 phosphate dehydrogenase as alternate electron sinks when carbon fixation diminishes and (ii) ferrodoxin as a regulator of redox flux between major metabolic pathways (Chowdhury et al., 2022). Thus, the robustness of *R. palustris'* H_2 production arsenal provides a platform for developing overproducing strains and for generating a more complete understanding of H_2 production by photosynthetic bacteria in general.

R. palustris is an attractive microbial biocatalyst for commercial hydrogen production since it can generate ATP from light and reductant necessary for nitrogen fixation from a wide variety of compounds including aromatic compounds (Alsiyabi et al., 2021; Archana et al., 2003; Fiβler et al., 1995), inorganic electron donors (e.g. thiosulfate) (Huang et al., 2010), industrial wastes (Adessi et al., 2018; Corneli et al., 2017; Lee et al., 2011, 2006; Pintucci et al., 2015, 2013), substrates with relatively high salt concentrations (Adessi et al., 2016b), and carbon monoxide and water (Oh et al., 2005). For example, *R. palustris* has been shown to produce biohydrogen from crude glycerol (a byproduct of biodiesel manufacturing) to yields higher than other photosynthetic bacteria (Ghosh et al., 2012; Sabourin-Provost and Hallenbeck, 2009). Strains P4 and PT can grow to a higher cell density, have a high specific H_2 production activity, and generate carbon monoxide-dependent H_2 production from the water-gas shift reaction (Hosseini et al., 2015; Oh et al., 2005, 2002). Perhaps the most promising biohydrogen production strategy thus far has been syntrophic metabolism of co-cultures. Table 2 provides an overview of some highlighted H_2 production systems involving *R. palustris*. Developing co-culture systems employing *R. palustris* enables the removal of inhibitory compounds or metabolic byproducts by *R. palustris* that other microbes could not catabolize, improves biomass production of the organism(s), and fosters more complete consumption of feedstocks. Several co-culture systems have developed relatively high H_2 yields utilizing a combined dark-photo fermentation process from potato starch and glucose (Hitit et al., 2017c), cellulose (Hitit et al., 2017a), cheese whey (Azbar and Cetinkaya Dokgoz, 2010), cassava starch (Su et al., 2009a, 2009b), and bread waste (Adessi et al., 2018). Yet, more research and development regarding H_2 production from renewable and cost-effective substrates is necessary. Lignocellulosic biomass has high potential as an ideal feedstock for photofermentative H_2 production. *R. palustris* shows resistance towards high phenolic concentrations derived from lignocellulosic biomass and has been known to utilize lignin breakdown productions for H_2 production (Alsiyabi et al., 2021; Mabutyana and Pott, 2021). Advances in co-culture systems with lignocellulosic biomass whereby one organism consumes the sugars and *R. palustris* utilizes the inhibitory phenolic compounds could further valorize biohydrogen production from lignocellulosic biomass.

There have been numerous progressive techniques engineered for biohydrogen production involving *R. palustris*. Entrapment of cells in gels (Ross and Pott, 2021; Tian et al., 2009; Wang et al., 2013), support mediums like grid columnar flat panels (Wang et al., 2019b), SiO_2-chitosan support mediums (Liao et al., 2013), and reverse micelles (Pandey et al., 2007) have shown improved H_2 production compared to planktonic cultures. Biofilm photobioreactors using packed glass beads (Tian et al., 2010) and optical fiber-illuminating photobioreactors (Chen et al., 2006a) have shown promise as well. *R. palustris* has also been sed as a model organism for testing continuous reactors and for employing ultrasonic treatment to boost H_2 production (Wang et al., 2012). Several

Table 2
Highlighted examples of biohydrogen production systems with *R. palustris*.

	Organism(s)	Substrate(s)	Total H_2 (mol H_2/mol substrate)	Notes	Reference(s)
Single Stage	*R. palustris* CGA009	Polyester substrate coating (reductant)	8.24	Nongrowing cells coated and stabilized with a novel latex coating	(Gosse et al., 2010; Piskorska et al., 2013)
	Clostridium butyricum CGS55 and *R. palustris* CGA009	Potato starch and glucose	6.4	Dark-photo fermentation; response surface methodology with a Box-Behnken design was used to optimize	(Hitit et al., 2017c)
	R. palustris CGA009	Glycerol	6.69	Stoichiometric conversion of biodiesel derived crude glycerol; Simpler operation; suitable for metabolism study; substrates limited to a few sugars and some organic acids	(Ghosh et al., 2012; Pott et al., 2014; Sabourin-Provost and Hallenbeck, 2009; Zhang et al., 2015)
	R. palustris CGA009	Butyrate	4.92	Incandescent light was found to be more effective	(Hu et al., 2018)
	R. palustris CGA009 and *Cellulomonas fimi*	Cellulose (glucose)	3.84	Effective H_2 production from cellulose by co-cultures without previous pre-treatment	(Hitit et al., 2017a)
	R. palustris CGA009	Ethanol	2.0	Optimized by response surface methodology	(Liu et al., 2015)
Two Stage	*Mixed culture with R. palustris DSM 127*	Cheese whey (lactose)	10	Combined dark-photo fermentation process	(Azbar and Cetinkaya Dokgoz, 2010)
	Thermotoga neapolitana DSM 4359^T and *R. palustris* 42OL	Glucose	9.4	Combined dark-photo fermentation process; Broad substrate range; addition operational cost from treatment of fermentation effluents of first stage	(Dipasquale et al., 2015)
	Clostridium butyricum CGS55 and *R. palustris* WP3–5	Sucrose	5.6	Sequential dark-photo fermentation and autotrophic microbial growth for high yield and CO_2-free biohydrogen production	(Lo et al., 2010)
	Lactobacillus amylovorus DSM 20532 and *R. palustris 42OL*	Bread waste (glucose)	3.1	Sequential lactic and photo-fermentation; among the highest yields obtained on starch containing substrates; No hydrolytic pretreatment necessary	(Adessi et al., 2018)
	R. palustris P4	Acetate	2.8	Combined dark-photo fermentation process	(Oh et al., 2004; Padovani et al., 2016)
	Klebsiella sp. TR17 and *R. palustris* TN1	Glycerol	0.8	Combined dark-photo fermentation process of crude glycerol	(Chookaew et al., 2015)
Semi-Continuous or Continuous	*R. palustris* GCA009	Acetate	3.15	Optical-fiber-assisted illumination systems	(Chen et al., 2006b)
	R. palustris 42OL	Malic acid	3.03	High irradiance under a semicontinuous regime	(Carlozzi, 2012)
	R. palustris GCA009	Glucose	1.15	Grid columnar flat panel photobioreactor with immobilized cells	(Wang et al., 2019b)

modeling techniques such as statistical experimental design (Jamil et al., 2009), response surface methodology, and desirability function approaches (Hitit et al., 2017a, 2017b; Liu et al., 2015; Shi et al., 2014) have optimized H_2 production by *R. palustris* in a variety of conditions. A method of using light-activated materials and biocatalysts from *R. palustris* to produce H_2 with conjugated polymers has been developed recently (Wang et al., 2021). Plasmonic nanoparticles and near-infrared light offer a novel method for conversion of organic acids to H_2 by *R. palustris* and increased the purity of H_2 produced (Craven et al., 2019). A nanoscale organic-iron complex was shown to be more efficient than iron ions alone, and improved H_2 production in several strains of *R. palustris* (Kanwal et al., 2020). Sustained outdoor biohydrogen production from tubular photobioreactors has also been demonstrated (Adessi et al., 2012). Lastly, acclimation strategies like photo-acclimation (Muzziotti et al., 2017), photo-evolution (Pintucci et al., 2015), and heat-acclimation (du Toit and Pott, 2021) have generated new strains with significantly improved H_2 production.

In summary, *R. palustris* is a robust and diverse powerhouse for biohydrogen production (Fig. 3). However, there is still room for growth to further valorize biohydrogen generation for industrial-scale production. The main bottleneck of H_2 production is production efficiency, and either sequential or co-culture systems offer a possibility to boost efficiency. A combination of dark and photo-fermentation may be the solution to converting organic acids, removing chemical oxygen demand, and enabling more flexibility for using renewable and cheaper feedstocks. Furthermore, the photofermentation production aspect of the system needs to be optimized to increase the lower growth rates of the photosynthetic bacteria as well as boosting light conversion efficiencies. Genetically engineering *R. palustris* to optimize H_2 production at various light intensities, reducing the lag phase, and increase H_2 production rates are all examples of ways to boost production in a combined dark and photo-fermentative system (Kour et al., 2019). Combined dark and photofermentative H_2 production from wastes (e.g. waste waters and lignocellulosic biomass) provide a unique opportunity to utilize cheap and renewable feedstocks in which more complete conversion can be accomplished by multiple organisms.

Apart from biohydrogen production, lipids offer a potential alternative to petroleum-based products, and several studies have aimed at characterizing *R. palustris*' lipid metabolism. For example, *R. palustris* has been employed to study the role of protein phosphorylation in lipid production, revealing that pyruvate phosphate dikinase (PPDK, RPA1051) could be a key protein to more efficiently produce biodiesel material in the future (Hu et al., 2012). Strain TIE-1 has also been employed to remodel lipid production via the loss of hopanoids and hopanoid methylation, showing that lipid production by a microbe varies with growth conditions and even with the loss of particular genes (Neubauer et al., 2015). However, there is still a large need to characterize the regulatory mechanisms of lipid production under different growth conditions by *R. palustris* in order to foster more efficient and industrial-scale production as a biofuel.

5. *R. palustris* for electricity generation

Bioelectrochemical systems have emerged as a promising means for developing sustainable electricity generation, waste removal, recovering valuable resources, and producing chemicals (Bajracharya et al., 2016). These systems utilize microbes as biocatalysts to convert chemical energy into electrical energy (and vice versa) and rely on the ability

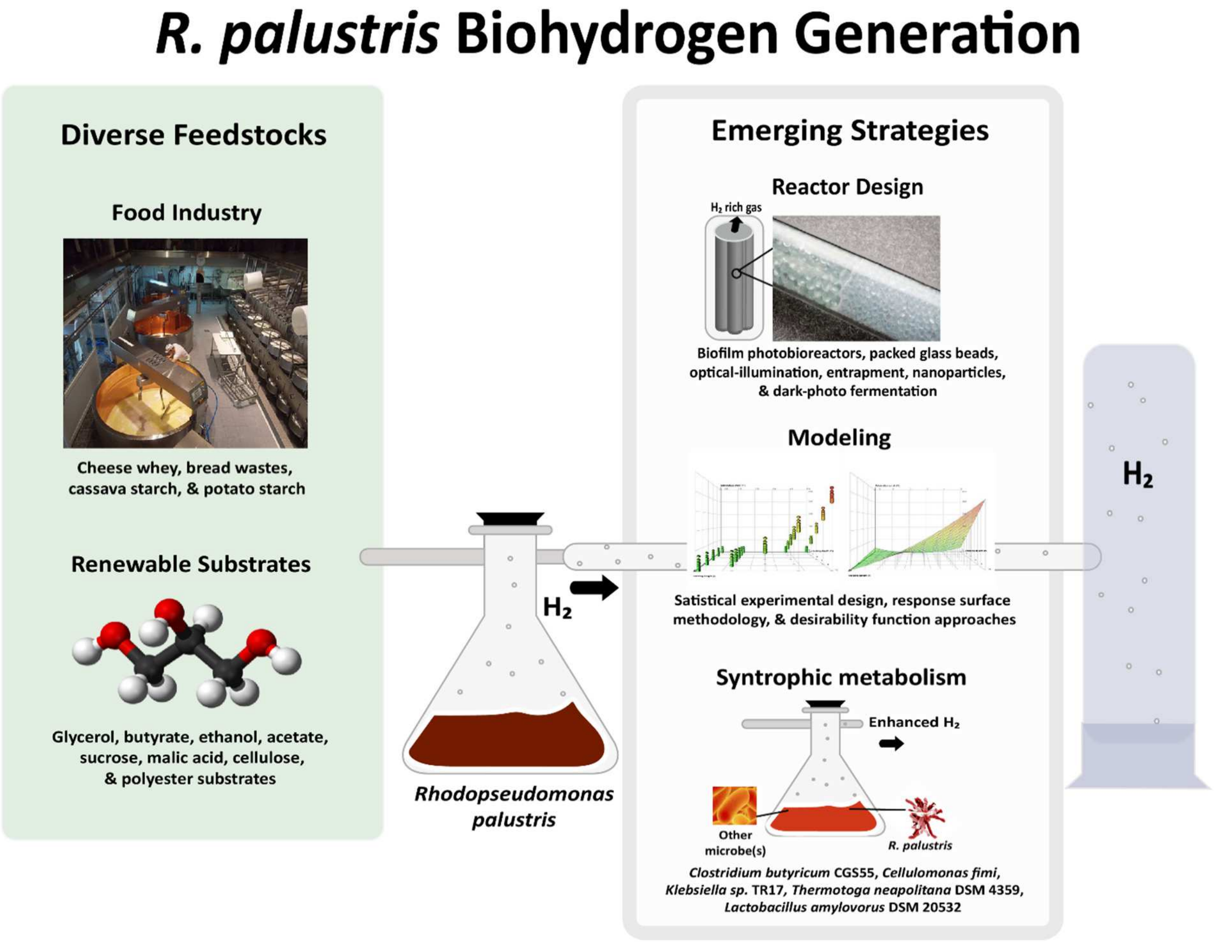

Fig. 3. Highlights of biohydrogen production by *R. palustris* from versatile feedstocks and novel strategies for enhancement.

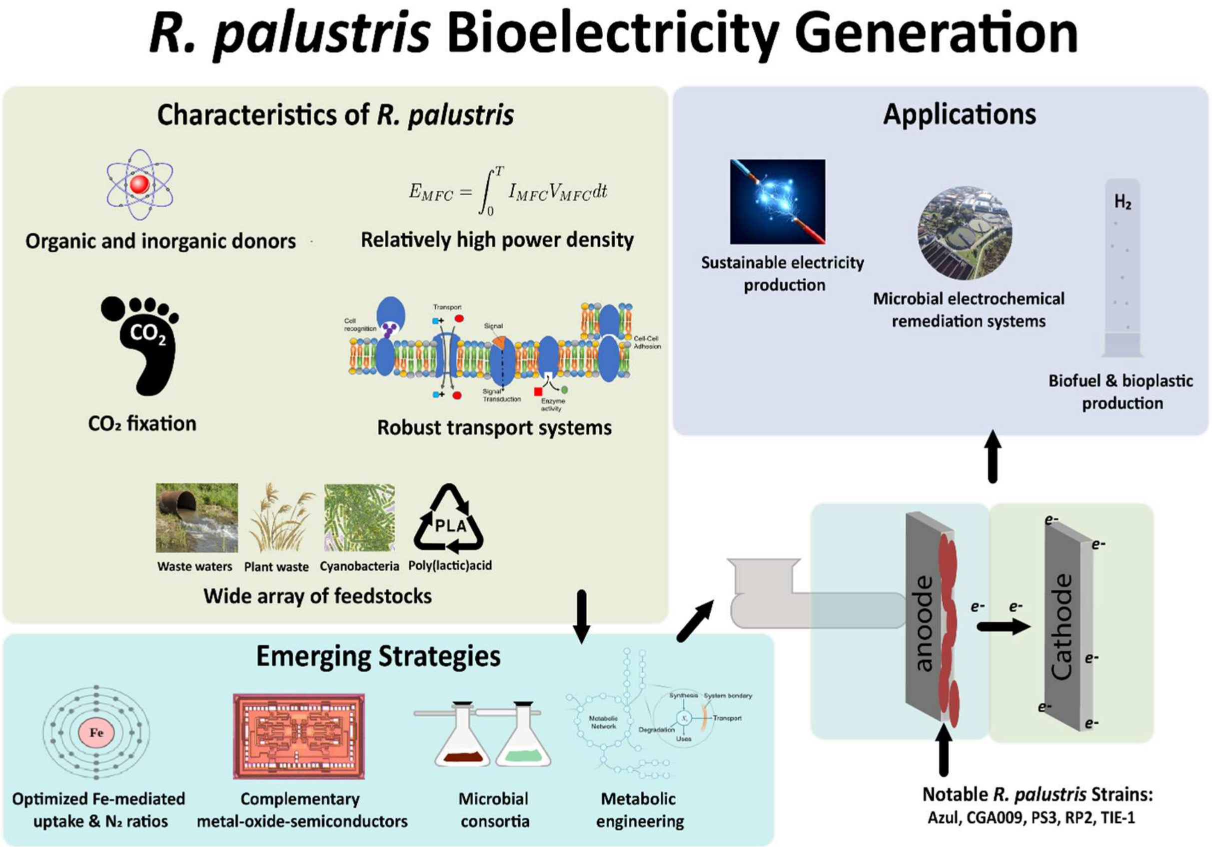

Fig. 4. Electricity generation by *R. palustris*. Due to its flexible and robust metabolism, several types of bioelectrochemical systems involving *R. palustris* have been engineered, which can utilize renewable feedstocks for the generation of power and other applications.

of the microbe to transport electrons. As a facultative phototroph, *R. palustris* offers distinct advantages regarding engineering toward more efficient bioelectrical systems (Fig. 4). Under photoautotrophic conditions, *R. palustris* utilizes electrons from inorganic donors to generate reducing equivalents. However, under photoheterotrophic conditions *R. palustris* can obtain these electrons from organic donors and balances the excess reducing power through CO_2 fixation or via other electron acceptors (Fig. 2). Thus, its flexible metabolism enables it to either accept or supply electrons to an electrode. For example, *R. palustris* Azul can perform direct and indirect electron uptake during phototrophic conditions, flexibly taking electrons from a cathode or using an anode as an electron sink (Guardia et al., 2020). While many organisms can use soluble oxidants and reductants, *R. palustris* can also access solid-phase materials for more flexible bioelectrochemical generation. Strain TIE-1 has served as model photoferrotroph, revealing a previously unknown ability to use extracellular electron transfer for electron uptake (Bose et al., 2014). Building upon this knowledge, Guzman et al. (2019) discovered that electrons from extracellular uptake enter the photosynthetic electron transport chain. Deletion of the genes encoding Rubisco in *R. palustris* TIE-1 led to a reduction in extracellular electron uptake, which highlights that phototrophic electron uptake is linked to CO_2 fixation (Guzman et al., 2019). This demonstrates that phototrophs can directly use solid-phase substances for electron transfer, energy transduction, and CO_2 fixation. Consequently, *R. palustris* was the first purple non-sulfur bacterium demonstrated to perform direct contact and electron transfer following biofilm growth. Strain TIE-1 has also been studied to gain a more fundamental insight into how phototrophs utilize ferrous iron as an electron donor to fix carbon dioxide using light energy, which revealed that they employ unique protein complexes made of outer membrane porins and electron transfer proteins to harvest electrons (also known as the PioAB electron conduit) (Dinesh et al., 2022). Fundamental insights like this can be useful for improving electron uptake ability and growth under photoelectroautotrophic conditions by iron-mediated uptake strategies like the addition of immobilized iron-based mediators (e.g. Prussian Blue) (Doud and Angenent, 2014; Rengasamy et al., 2018). In general, *R. palustris* shows great promise as a bioelectrochemical chassis due to the headway made in fundamental research, its ability to generate electricity at higher power density relative to mixed cultures, and its robust metabolism that can consume a wide variety of substrates (Xing et al., 2008). Progress in our fundamental understandings of how *R. palustris* generates electricity has fostered an array of diverse and exciting applications.

Microbial fuel cells (MFCs) are a type of bioelectrochemical system where heterotrophic bacteria metabolize exogenous organic nutrients and generate external electrical currents (Howe and Bombelli, 2020). Comparatively, in biophotovoltaics (BPVs) the electrical current comes from electrons generated by the light-driven oxidation of water that are passed through the photosynthetic electron transfer chain (rather than via heterotrophic metabolism) (Howe and Bombelli, 2020). Sometimes referred to as photosynthetic microbial fuel cells (photo-MFCs), BPVs do not require supply of an added organic substrate like MFCs, and thus mass transfer is not a limiting factor of BPVs. *R. palustris* has been applied in MFCs and photo-MFCs using corn stover (Wang et al., 2009), rice paddy soils (Liu et al., 2021), poly(lactic)acid (Qi et al., 2018b, 2018a), and whole-cell cyanobacteria (Inglesby et al., 2012) as feedstocks. The essential factors affecting bioelectricity generation have been illuminated, showcasing that improved power performance arises from CO_2 fixation, oxidation of ferrous iron, and the biofilm acting as a living electrode in the system. Complementary metal-oxide-semiconductor technology also showed promise, which is expected to deliver a potentially lower-cost system with higher power output for practical applications. In another study, a portable paper-based MFC was fabricated using *R. palustris*, which could be preserved for long-term usage with only 10% performance degradation after four weeks (Otani et al., 2020). *R. palustris* has also been applied in MFCs employing microbial electrochemical remediation systems (MERS), strategies that exploit microorganisms' abilities for remediation (e.g. treating contaminants) in the environment while also producing electricity. Strain RP2 was isolated from anodic biofilms of MERS and has the capability for direct electrode respiration, anaerobic nitrate reduction, dissimilarity metal oxide reduction, and degradation of petroleum hydrocarbons (Venkidusamy and Megharaj, 2016). However, despite the advances in bioelectrochemical production with *R. palustris* there are several challenges that impede industrial-scale applications.

Scaling up MFC systems for practical application requires significantly increasing the size of the reactors, simultaneously maintaining constant energy output per unit volume, enhancing operational stability, reducing corrosion, and optimizing biofilm formations with co-cultures of electrochemically active bacteria (Jadhav et al., 2021; Pandit et al., 2020). When comparing factors that affect bioelectricity generation by *R. palustris*, metabolic activity mainly determines the performance of power and energy outputs compared to other factors in the MFC like nutritive substances (e.g. soil, lignocellulosic biomass, acetate) (Liu et al., 2021) Thus, focusing efforts to regulate bioelectricity generation from a systems level could provide a solution for improved performance for scale-up. For example, suppressing hydrogen production renders more availability to reducing equivalents, thereby improving electricity generation by *R. palustris* (Morishima et al., 2007). Genetic engineering initiatives that manipulate electron conduits for extracellular electron uptake (e.g. PioAB) could help improve electron harvesting from both soluble iron and poised electrodes and improve yields (Dinesh et al., 2022). Emerging techniques in metabolic modeling also show promise for *in silico* analysis of metabolic regulation for redox balance in *R. palustris* (Alsiyabi et al., 2021, 2019; Chowdhury et al., 2022). Further characterization of electron uptake mechanisms is required for future biotechnology efforts, such as extracellular electron shuttles that help subpopulations of biofilms maintain metabolic activity (Saunders et al., 2020). *R. palustris'* genome has an arsenal of electron transport mechanisms that have yet to be explored in great detail, like the porin-cytochrome complexes that facilitate movement of electron acceptors (e.g. MtrA/MtrB cytochrome: porin homologues MtoA/MtoB) (Larimer et al., 2004; McCormick et al., 2015). Another avenue for improving bioelectrochemical potential is to manipulate iron storage capabilities, which could possibly be achieved through genetic engineering of *R. palustris'* ferrosomes, a new class of lipid-bounded iron storage organelles that likely help manage adaptation to iron starvation (Grant and Komeili, 2020). More studies are necessary to codify molecular mechanisms, discover associated genetic determinants, and examine how electron uptake from solid-phase electron donors impacts other cellular metabolic pathways. Reactor design with emerging techniques can also facilitate more efficient systems and promote the ability for commercialization. Stacking of tubular MFCs is a proposed technoeconomic solution for upscaling, and thus future efforts could examine stacked systems with *R. palustris* (Rikame et al., 2022). Further optimizing systems with nanomaterials is also a promising route, such as with metals (e.g. Au, Pd, Cd), carbon-based nanomaterials (e.g. graphene, carbon nanotubes), coatings and conjugated nanoparticles (e.g. poly(3,4-ethylenedioxyophene, polyaniline, and polypyrrole) (Mouhib et al., 2019) It has also been shown recently that the nitrogen ratio can be customized to manipulate the fraction of electron flux directed toward biosynthesis, biohydrogen, and extracellular electron transfer (Pankan et al., 2020). Syntropy between microbial consortia of *R. palustris* and hydrogen oxidizing bacteria has also been proposed as a strategy to produce higher power densities in MFCs (Park et al., 2014). Ultimately, advances in our understanding of the critical components and mechanisms factored into electrochemical production, the development of improved genetic tools, and initiatives in scale-up feasibility should progress the possibilities of utilizing *R. palustris* as a versatile platform for power production, especially from cheaper and renewable feedstocks like wastes or lignocellulosic biomass.

6. *R. palustris* for bioplastic production

Since the 1950s, an estimated 18.2 trillion tons of fossil-fuel derived plastics have been created, with only 9% of it being recycled (Geyer et al., 2017). Thus, there has been much attention paid to finding sustainable and renewable alternatives to conventional plastics. Polyhydroxyalkonoates (PHAs) are a type of biopolymer created by a variety of microbes under certain environmental conditions that are stored as granules inside the cell. PHAs are an ideal substitute for conventional plastics since they are biodegradable, renewable, biocompatible, have a wide range of diverse structures, and can be produced by a wide array of microorganisms (Chen et al., 2020a). Unfortunately, the widespread adoption of PHAs is hampered by higher production costs, which is largely attributed to feedstock costs (Chen et al., 2020a). Due to *R. palustris'* flexible metabolism and ability to utilize a wide array of feedstocks, it offers a unique opportunity to generate bioplastics from cheaper feedstocks and render PHAs more cost-effective for market acceptance.

R. palustris has been shown to produce PHAs from waste products, such as lignocellulosic biomass (Fig. 5). For example, *R. palustris* accumulates the most common PHA, called poly-3-hydroxybutyrate (PHB), from several lignin breakdown products (Alsiyabi et al., 2021; Brown et al., 2020) and nutrient recovery from cyanobacteria blooms (Tian et al., 2017). It has also been revealed that *R. palustris* is capable of creating a copolymer of PHB called poly-3-hydroxybutyrate-*co*-hydroxyvalerate (PHBV) that has better thermomechanical properties compared to PHB alone (Alsiyabi et al., 2021). Phasins are the dominant protein surrounding PHA granules inside bacteria, and our recent study expressed the dominant phasin from the PHB-producing model bacterium *Cupriavidus necator* H16 into *R. palustris* for the overproduction of PHB on lignin breakdown products (Brown et al., 2022). Thus, this foundation for bioplastic production by *R. palustris* from waste products like lignocellulosic biomass provides a steppingstone toward industrial production.

As previously described, there are tradeoffs in utilizing reducing power between biomass, PHA, and H_2 production by *R. palustris* (Chen et al., 2012; McKinlay et al., 2014; Touloupakis et al., 2021), and identifying how to capitalize on these tradeoffs is critical for engineering overproducing strains. A recent study delivered a synergistic experimental and computational biology approach that identified key design strategies for PHB overproduction in *R. palustris* and other organisms with similar metabolisms (Alsiyabi et al., 2021). Combined experimental results including PHB production on various substrates (e.g., lignin breakdown products), H_2 production, and electron microscopy suggested that the rate of PHB production is mainly controlled by metabolic factors. Thermokinetic analysis identified a bottleneck in the thiolase reaction (*phaA*) in the PHB production pathway. Application of a novel genome-scale metabolic model rendered four major findings including (i) a very high acetyl-CoA/CoA ratio is required to drive the thiolase reaction, (ii) substrates with high carbon uptake rates accumulate higher amounts of acyl-CoA, (iii) the rate through PhaB (reductase) is linearly dependent on the NADPH/NADP ratio, and (iv) PhaB will likely be rate-limiting even under optimal metabolic conditions due to its very low catalytic efficiency (Alsiyabi et al., 2021, 2019). Ultimately, *R. palustris* was used as a model organism for deciphering generalized design strategies that could be expanded to other organisms with similar metabolism for the over-production of PHB. Emerging techniques with microbial electrosynthesis have also capitalized on tradeoffs between PHB and H_2 production from available reducing potential. The ability to produce PHB by *R. palustris* TIE-1 via bioelectrochemical generation became the first study to systematically quantify PHB production by photoelectroautotrophy and

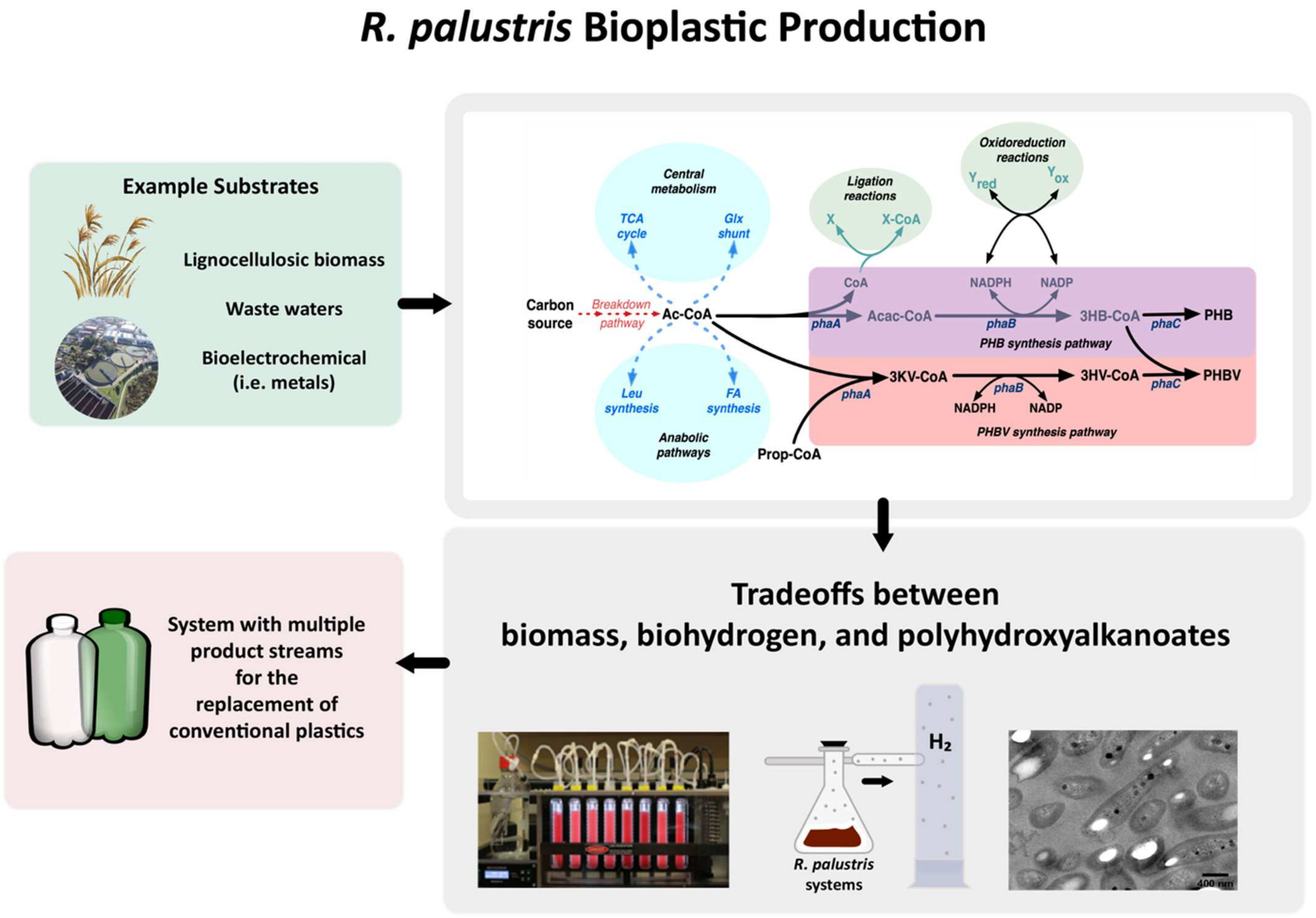

Fig. 5. Bioplastic production by the metabolically versatile *R. palustris*. It can produce monomers and copolymers of polyhydroxyalkanoates from various renewable and sustainable feedstocks. Its ability to produce several co-product streams also make *R. palustris* an ideal candidate for engineering toward industrial production.

photoferrautotrophy (Ranaivoarisoa et al., 2019). Other studies employing TIE-1 have utilized immobilized iron complexes and magnetite nanoparticle anchored graphene cathodes to enhance PHB production vial microbial electrosynthesis (Rengasamy et al., 2020, 2018).

Despite these advances in bioplastic production from *R. palustris*, many studies focus on H_2 production rather than PHA production due to its native ability as a powerhouse for biohydrogen generation. *R. palustris* is still emerging as a non-model bacterium for bioplastic production, and thus there are gaps in our understanding regarding its PHA production mechanisms. For example, characterizing *R. palustris'* native granule-associated-proteins (e.g phasins) employed for PHA production or engineering methods for increased fractions of valerate in PHBV production are ideal steppingstones.

7. *R. palustris'* environmental remediation and agricultural production

As a naturally occurring bacterium found in a wide variety of environments, *R. palustris* has been used as a bio-based method for applications in agriculture for bioremediation and to boost plant production. Industrial and agricultural activity can often be detrimental to soils and other environments, making it necessary to find effective and sustainable remediation methods. Bioremediation of contaminated soils has been demonstrated by several strains such as degradation of chlorobenzoic acids by strain RCB100 (Haq and Fixen, 2021), removal of heavy metals and metalloids by strain CGA009 (Batool et al., 2017; Llorens et al., 2012; Zhao et al., 2015), and elimination of acrylamide by strain Ac1 (Wampler and Ensign, 2005). Several strains of *R. palustris* have been applied for wastewater treatment and nutrient recovery for detoxifying pesticides (Luo et al., 2018; Wu et al., 2019; Yin et al., 2012a), removing halogenated compounds (Mutharasaiah et al., 2012), decreasing the chemical oxygen demand, nitrates, and H_2S in the system (Bogarapu et al., 2019), and cleaning aquaculture pond waters (Xiao et al., 2020). A shift from employing monocultures for bioremediation to microbial communities using advanced techniques like machine learning are enabling artificial selection of optimal consortia that can be applied in certain conditions (Borchert et al., 2021). Future efforts employing optimized systems of microbial consortia could further improve microbial remediation of wastewater and even promote the production of high-value products (Nagadomi et al., 2000).

With the increase in global population, the need to find more effective and sustainable methods to feed the growing population is ever pressing. Agricultural biostimulants have emerged as an ideal method for using biologically derived fertilizer additives or other products that are applied to boost plant health, growth, and productivity during crop production. *R. palustris* has shown great promise as a commercialized biostimulant for enhancing agricultural production. Notably, strain ELI 1980 has been used as a component of Quantum Light, a biofertilizer commercialized by Ecological Laboratories, Inc. (FL, USA) (Crovadore et al., 2017). A recent review on purple non-sulfur bacteria and plant production provides a nice overview of the many benefits several strains of *R. palustris* have had for numerous crops (Sakarika et al., 2020). Strains P3 and BCRC16408 have a promoting effect on *Brassica rapa chinensis* (Chinese cabbage) with reduced fertilizer input, the ability to use poorer-quality seeds, and higher crop yields (Hsu et al., 2021; Wong et al., 2014). A strategy for quicker and cheaper fermentation of strain P3 using corn steep liquor and molasses has also been developed, which further promotes it for large-scale industrial production (Lo et al., 2020). Strain GJ-22 yielded systemic protection of tobacco plants against tobacco mosaic virus (Su et al., 2017), and a genetic tool was developed recently enabling visualization of bacterial colonization on tobacco and rice leaves (Zhai et al., 2019). Stevia plants (Wu et al., 2013; Xu et al., 2018) and Chinese Dwarf Cherry seedlings (Yin et al., 2012b) are also among the plants known to have positive effects from *R. palustris*. Several strains of *R. palustris* have potential for biofertilizers for rice production as well. Strain PSB06 promotes rice growth and enhances stress resistance at the seedling stage, and both strain PSB06 and strain CGA006 increase the length of stems (Luo et al., 2019). Strains TK103, PP803, and P1 have several beneficial attributes to rice production including increased rice grain yield, significant reduction of inhibitory compounds via increasing 5-aminolevulinic acid production, increased root dry weight, and increased plant height under salt stress (Kantachote et al., 2016; Kantha et al., 2015). *R. palustris* also shows potential as a biofertilizer for plant growth at sites with heavy metal contamination, as demonstrated in with Strain CS2 on *Vigna mungo* (mung bean) in soil contaminated with arsenic and heavy metals (Batool et al., 2017).

Hence, *R. palustris* has been investigated and applied in a variety of biostimulant applications. However, deciphering the implications for abiotic stress tolerance, agronomic and physiological traits of crops, interaction with non-microbial biostimulants, and improvements in nutrient usage associated with *R. palustris* are all necessary to continue to develop it as a commercialized biostimulant (Rouphael and Colla, 2020).

8. Controlling *R. palustris*' unique metabolism

A major factor impeding the development of *R. palustris* as a biotechnology chassis is the lack of genetic toolkits and synthetic biology advances for this metabolically versatile, non-model microbe. Genetic engineering of *R. palustris* is lagging in part due to its innate resistance to antibiotics (Larimer et al., 2004), difficulty expressing transient genes from non-native plasmids, the lack of testing genetic parts, genetic redundancy, complications using fluorescent reporters in pigmented bacteria, relatively high G + C content of its genome, and gaps in our understanding of its gene expression mechanisms (e.g. origins of replication). Knockouts of specific cassettes or pathways have been achieved, including squalene and *n*-butanol production (Doud et al., 2017; Xu et al., 2016), investigating quorum sensing mechanisms (Hidetada et al., 2012b), and Rubisco deletions to explore extracellular electron uptake (Joshi et al., 2009). Insertions have proven more difficult, generally involving non-native plasmids with inefficient promoters that result in transient heterologous expression (du Toit et al., 2021). Although native plasmids have been isolated from some strains and used as vectors, their expression performance wanes in comparison to non-native plasmids (Inui et al., 2000).Thus, there is a significant need to characterize and develop native genetic engineering tools for *R. palustris*.

Recently, Immethun et al. (2022) had a breakthrough in progress toward forming baseline understandings of the behavior of key genetic parts to render more efficient engineering of this non-model microbe and developed tools to advance stable heterologous gene expression in *R. palustris*. This team characterized gene expression and plasmid maintenance for various selection markers, developed a synthetic biology toolbox with a number of tools (e.g. origins of replication, terminators, fluorescent reporters, and untranslated regions), and employed *R. palustris'* endogenous plasmid for exogenous protein production. These findings provide a better working foundation for heterologous protein production by *R. palustris* as a potential industrial biocatalyst.

Genomic insertions with chromosomal integration will also likely provide a means for more stable and long-term expression with reduced maintenance (i.e. limited antibiotics), decreased production costs, and improved potential for industrial scale applications. However, chromosomal modifications have been challenging and intermittent for *R. palustris* (Hidetada et al., 2012; Jackson et al., 2018; Rey et al., 2007). du Toit et al. (2021) innovated an optimized genetic toolset for rapid, markerless modification in *R. palustris* and employed optimized methods for the overexpression of alternative nitrogenase isoenzymes for superior biohydrogen production. To overexpress alternative *vnf* and *anf* nitrogenases, genes associated with biohydrogen production, the *pucBa* promoter was carefully chosen as a relatively strong promoter based on transcriptomics analysis. Plasmids were created to insert the promoters directly upstream of three putative nitrogenase operons to foster expression of necessary components. Since *R. palustris'* native vanadium nitrogenase genes do not have a single cluster, a synthetic codon-optimized *vnfH* gene was co-inserted with the promoter to create a unified vanadium nitrogenase operon. Electroporation parameters were also optimized to allow more efficient insertional mutagenesis, which included adjusting field strength (voltage), pulse duration (resistance), and optimal post-incubation conditions. This optimization allowed relatively large insertion sizes of the constructs to be integrated with similar efficiency as promoter-only insertions in about half the time as previously unoptimized methods. Lastly, this team developed a more efficient RNA extraction method for more accurate analysis of gene expression that reduced degradation and increased purity and yield. In the end, this system achieved chromosomal integration under a strong promoter and provides the means to repeatedly manipulate different genes without persistent selection markers.

Despite the recent advancements in genetic tools catered to *R. palustris*, significant work is necessary to flexibly and reliably utilize its unique metabolic capabilities. Characterization of plasmid origins of replication, functional promoter sequences (constitutive and inducible), ribosomal binding sites, terminators, potential downstream control regions of desired genes, post-transcriptional control, and a more fundamental insight into antibiotic resistance genes is essential. Moreover, realization of *R. palustris'* robust metabolism is still hampered by the lack of quick and efficient genetic engineering techniques, such as employing CRISPR-Cas (clustered regularly interspaced short palindromic repeats, CRISPR-associated) systems that have been widely applied for precise RNA-mediated metabolic engineering in other microbes. Although Type II-C Cas9 endonucleases have been identified for *R. palustris* BisB5 and BisB18 (Chylinski et al., 2013; Ma et al., 2015), this class of Cas9 system has a weak DNA helicase, limited dsDNA binding and unwinding activity, and promiscuous guide RNA specificity compared to the widely used Type II-A Cas9 systems. Nonetheless, Type II-C Cas9 systems are generally the simplest of the systems and the ability to employ this Cas9 system could provide more options for controlling this robust microbe. Developing CRISPR systems for specific use in *R. palustris*, such as CRISPR-d Cas9 programmable repressors, could enable metabolic flux for the overproduction of industrially relevant products (e.g. bioelectricity, biohydrogen, or bioplastics). Advances in reliable genetic engineering techniques coupled with omics and genome-scale metabolic modeling initiatives will likely render the ability to better control *R. palustris*' robust metabolic capabilities in the future, particularly regarding its innate redox imbalance under photoheterotrophic growth and the wide range of potential bioconversion pathways.

9. *R. palustris* and circular economies

There is a global shift in policies and regulations to minimize waste generation and its associated environmental impact, and circular bioeconomies offer a sustainable solution. *R. palustris'* robust metabolism and ability to consume a wide variety of waste products like lignocellulosic biomass, wastewater sludge, and spent foods render it an ideal candidate to generate circular bioeconomies via the production of biofuels, biofertilizers, chemicals, proteins, and other industrially relevant products.

The waste-to-energy nexus for circular economies and environmental protection is perhaps one of the largest potential applications with *R. palustris* due to the headway made in the biohydrogen and bioenergy sectors (Sharma et al., 2020). Unfortunately, biohydrogen production is still not cost-competitive compared to traditional approaches. Dark fermentation systems are not efficient enough at converting organic materials to biohydrogen, but implementing combined dark and photofermentation systems for biohydrogen production from waste products can help improve efficiency. Single-stage dark and photofermentation systems for biohydrogen production allow for combined fermentation (i.e. co-cultures) in a single reactor and are simpler to operate than many other systems (e.g. no dilution steps required). Creating modular single-stage combined fermentation systems that can easily be established near locally sourced waste supplies could economically generate biohydrogen from wastes with *R. palustris*. Similarly, *R. palustris* could be employed for bioelectricity generation from organic wastes via microbial fuel cells that can be established near waste sources and even provide solutions to off-grid communities. Spent biomass produced in the bioenergy production process could then be used as a protein source to further increase economic potential and promote circular economies, as demonstrated with the mass production of *R. palustris* as a protein source in aquaculture feed (Alloul et al., 2021; Kim and Lee, 2000; Zhang et al., 2013) or as a biofertilizer (Wong et al., 2014). Learning from bottlenecks and challenges in microalga biorefineries, when hyperaccumulation of the target product is still not economically feasible there can be a shift toward co-producing several compounds (Gifuni et al., 2019). Since there is generally competition between biohydrogen, bioplastic, and biomass production by *R. palustris*, operating integrated biorefineries to capitalize on several products streams from waste feedstocks could be ideal.

In the end, employing *R. palustris* to produce industrially relevant products from cheap and renewable feedstocks like wastes could provide a methodology for circular economies that reduces waste generation and management needs with less socioeconomic and environmental impacts. Implementing integrated waste biorefineries that combine biological, thermochemical, and chemical processing could provide higher conversion efficiencies and further promote the valorization of waste streams. Advances in genetic engineering tools should also foster the ability to flexibly control *R. palustris* for bioenergy or bioproduct production based on market demands.

10. Conclusions

R. palustris is a purple non-sulfur bacterium that is an attractive option as a biotechnology chassis since it is among the most metabolically robust bacteria, with the ability to catabolize a wide variety of feedstocks and turn them into several high-value products. Due to its versatile metabolism, *R. palustris* has been studied and applied in a wide variety of applications such as biodegradation of aromatic compounds, environmental remediation, biofuel production, agricultural biostimulation, and electricity production. Currently, biohydrogen production from wastes is perhaps the most feasible application due to the production capacity of *R. palustris*, headway made in fundamental research, genetic engineering initiatives, emerging techniques in reactor systems, demand for alternative fuels, and increasing desire to foster circular bioeconomies. Developing co-culture systems employing *R. palustris* enables the removal of inhibitory compounds or metabolic byproducts by *R. palustris* that other microbes could not catabolize, improves biomass production of the organism(s), and fosters more complete consumption of feedstocks. In particular, systems employing lignocellulosic biomass as feedstock could be ideal due to the innate resistance of *R. palustris* towards high phenolic concentrations derived from lignocellulosic biomass and its ability to utilize lignin breakdown productions for hydrogen production. From an economic and environmental sustainability perspective, multiple initiatives should be integrated into a single system, such as employing biodegradation of wastes for biohydrogen production and then subsequently using the generated biomass for protein feed in aquaculture systems. While *R. palustris* holds great potential for commercial applications, there are several key factors impeding current development.

Although *R. palustris* is capable of producing bioplastics from waste products like lignocellulosic biomass or wastewaters, the titers are not high enough to be commercially feasible from an economic standpoint compared to other microbes. Due to competition for reducing potential between biohydrogen, bioplastic, and biomass metabolic systems, eliminating pathways for bioplastic production can help funnel more reducing power for biohydrogen generation. More progress in genetic engineering discoveries and toolkits is needed to successfully control this metabolically robust microbe for the overproduction of targeted products for commercialization. Developing a deeper fundamental understanding of key regulatory systems in *R. palustris* is critical, such as further characterizing its robust transport systems. Ultimately, the commercial application of *R. palustris* as a versatile biotechnology chassis will continue to rise as advances in our understanding of systems-level tradeoffs in metabolic capacities are coupled with synthetic biology and emerging technologies that utilize renewable substrates.

CRediT authorship contribution statement

Brandi Brown: Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing – original draft, Resources, Data curation, Visualization. **Mark Wilkins:** Resources, Funding acquisition, Supervision, Writing – review & editing. **Rajib Saha:** Resources, Funding acquisition, Supervision, Writing – review & editing.

Declaration of Competing Interest

The authors report no conflict of interest.

Data availability

No data was used for the research described in the article.

Acknowledgments

We gratefully acknowledge funding support from National Science Foundation (NSF) CAREER grant (25-1106-0039-001), Nebraska Center for Energy Science and Research grants (26-1217-0020-403 and 26-1217-0020-413), and NSF EPSCoR Center for Root and Rhizobiome Innovation (CRRI) Grant (21-6262-4215).

References

Adessi, A., Concato, M., Sanchini, A., Rossi, F., De Philippis, R., 2016b. Hydrogen production under salt stress conditions by a freshwater *Rhodopseudomonas palustris* strain. Appl Microbiol Biotechnol 100, 2917–2926. https://doi.org/10.1007/s00253-016-7291-4.

Adessi, A., Spini, G., Presta, L., Mengoni, A., Viti, C., Giovannetti, L., Fani, R., De Philippis, R., 2016a. Draft genome sequence and overview of the purple non sulfur bacterium *Rhodopseudomonas palustris* 42OL. Stand. Genomic Sci. 11 https://doi.org/10.1186/s40793-016-0145-y.

Adessi, A., Torzillo, G., Baccetti, E., De Philippis, R., 2012. Sustained outdoor H_2 production with *Rhodopseudomonas palustris* cultures in a 50L tubular photobioreactor. Int. J. Hydrog. Energy 37, 8840–8849. https://doi.org/10.1016/j.ijhydene.2012.01.081.

Adessi, A., Venturi, M., Candeliere, F., Galli, V., Granchi, L., De Philippis, R., 2018. Bread wastes to energy: Sequential lactic and photo-fermentation for hydrogen production. Int. J. Hydrog. Energy 43, 9569–9576. https://doi.org/10.1016/j.ijhydene.2018.04.053.

Alloul, A., Wille, M., Lucenti, P., Bossier, P., Van Stappen, G., Vlaeminck, S.E., 2021. Purple bacteria as added-value protein ingredient in shrimp feed: *Penaeus vannamei* growth performance, and tolerance against Vibrio and ammonia stress. Aquaculture 530, 735788. https://doi.org/10.1016/j.aquaculture.2020.735788.

Alsiyabi, A., Immethun, C.M., Saha, R., 2019. Modeling the interplay between photosynthesis, CO_2 fixation, and the quinone pool in a purple non-sulfur bacterium. Sci. Rep. https://doi.org/10.1038/s41598-019-49079-z.

Alsiyabi, A., Brown, B., Immethun, C., Long, D., Wilkins, M., Saha, R., 2021. Synergistic experimental and computational approach identifies novel strategies for polyhydroxybutyrate overproduction. Metab. Eng. 68 https://doi.org/10.1016/j.ymben.2021.08.008.

Archana, A., Sasikala, C., Ramana, C.V., 2003. Augmentation of H_2 photoproduction in *Rhodopseudomonas palustris* by N-heterocyclic aromatic compounds. Biotechnol. Lett. 25, 79–82. https://doi.org/10.1023/A:1021717424268.

Austin, S., Kontur, W.S., Ulbrich, A., Oshlag, J.Z., Zhang, W., Higbee, A., Zhang, Y., Coon, J.J., Hodge, D.B., Donohue, T.J., Noguera, D.R., 2015. Metabolism of multiple aromatic compounds in corn stover hydrolysate by *Rhodopseudomonas palustris*. Environ. Sci. Technol. https://doi.org/10.1021/acs.est.5b02062.

Azbar, N., Cetinkaya Dokgoz, F.T., 2010. The effect of dilution and l-malic acid addition on bio-hydrogen production with *Rhodopseudomonas palustris* from effluent of an acidogenic anaerobic reactor. Int. J. Hydrog. Energy 35, 5028–5033. https://doi.org/10.1016/j.ijhydene.2009.10.044.

Bai, W., Ranaivoarisoa, T.O., Singh, R., Rengasamy, K., Bose, A., 2021. n-Butanol production by *Rhodopseudomonas palustris* TIE-1. Commun. Biol. 4, 1–16. https://doi.org/10.1038/s42003-021-02781-z.

Bajracharya, S., Sharma, M., Mohanakrishna, G., Dominguez Benneton, X., Strik, D.P.B.T. B., Sarma, P.M., Pant, D., 2016. An overview on emerging bioelectrochemical systems (BESs): Technology for sustainable electricity, waste remediation, resource recovery, chemical production and beyond. Renew. Energy 98, 153–170. https://doi.org/10.1016/j.renene.2016.03.002.

Banu, R., Kavitha, S., Yukesh Kannah, R., Poornima Devi, T., Gunasekaran, M., Kim, S.-H., Kumar, G., 2019. A review on biopolymer production via lignin valorization. Bioresour. Technol. 290, 121790 https://doi.org/10.1016/j.biortech.2019.121790.

Batool, K., Tuz Zahra, F., Rehman, Y., 2017. Arsenic-redox transformation and plant growth promotion by purple nonsulfur bacteria *Rhodopseudomonas palustris* CS2 and *Rhodopseudomonas faecalis* SS5. Biomed. Res. Int. 2017, 6250327. https://doi.org/10.1155/2017/6250327.

Berne, C., Allainmat, B., Garcia, D., 2005. Tributyl phosphate degradation by *Rhodopseudomonas palustris* and other photosynthetic bacteria. Biotechnol. Lett. 27, 561–566. https://doi.org/10.1007/s10529-005-2882-7.

Berne, C., Pignol, D., Lavergne, J., Garcia, D., 2007. CYP201A2, a cytochrome P450 from *Rhodopseudomonas palustris*, plays a key role in the biodegradation of tributyl phosphate. Appl. Microbiol. Biotechnol. 77, 135–144. https://doi.org/10.1007/s00253-007-1140-4.

Bisson, C., Salmon, R.C., West, L., Rafferty, J.B., Hitchcock, A., Thomas, G.H., Kelly, D.J., 2022. The structural basis for high-affinity uptake of lignin-derived aromatic compounds by proteobacterial TRAP transporters. FEBS J. 289, 436–456. https://doi.org/10.1111/febs.16156.

Bogarapu, R., Kumar, R., Madanapally, U.D., Nayak, J., 2019. Role of purple non-sulfur bacteria *Rhodopseudomonas palustris* RSOU000 and *Rhodopseudomonas thermotolerance* RSOU555 in waste water treatement. World J. Pharm. Pharm. Sci. 5, 1379–1387. https://doi.org/10.20959/wjpps20168-7428.

Borchert, E., Hammerschmidt, K., Hentschel, U., Deines, P., 2021. Enhancing microbial pollutant degradation by integrating eco-evolutionary principles with environmental biotechnology. Trends Microbiol. https://doi.org/10.1016/j.tim.2021.03.002.

Bose, A., Gardel, E.J., Vidoudez, C., Parra, E.A., Girguis, P.R., 2014. Electron uptake by iron-oxidizing phototrophic bacteria. Nat. Commun. 5, 3391. https://doi.org/10.1038/ncomms4391.

Brown, B., Immethun, C., Wilkins, M., Saha, R., 2020. *Rhodopseudomonas palustris* CGA009 polyhydroxybutyrate production from a lignin aromatic and quantification via flow cytometry. Bioresour. Technol. Rep. https://doi.org/10.1016/j.biteb.2020.100474.

Brown, B., Immethun, C., Alsiyabi, A., Long, D., Wilkins, M., Saha, R., 2022. Heterologous phasin expression in *Rhodopseudomonas palustris* CGA009 for bioplastic production from lignocellulosic biomass. Metab. Eng. Commun. 14 https://doi.org/10.1016/J.MEC.2021.E00191 e00191–e00191.

Carlozzi, P., 2012. Hydrogen photoproduction by *Rhodopseudomonas palustris* 42OL cultured at high irradiance under a semicontinuous regime. J. Biomed. Biotechnol. 2012, 590693 https://doi.org/10.1155/2012/590693.

Çelik, L., Ozturk, A., Abdullah, M.I., 2012. Biodegradation of reactive red 195 azo dye by the bacterium *Rhodopseudomonas palustris* 51ATA. Afr. J. Microbiol. Res. 6, 120–126. https://doi.org/10.5897/AJMR11.1059.

Chang, T.-H., Wang, R., Peng, Y.-H., Chou, T.-H., Li, Y.-J., Shih, Y., 2020. Biodegradation of hexabromocyclododecane by *Rhodopseudomonas palustris* YSC3 strain: A free-living nitrogen-fixing bacterium isolated in Taiwan. Chemosphere 246, 125621. https://doi.org/10.1016/j.chemosphere.2019.125621.

Chen, C.-Y., Lee, C.-M., Chang, J.-S., 2006a. Hydrogen production by indigenous photosynthetic bacterium *Rhodopseudomonas palustris* WP3–5 using optical fiber-illuminating photobioreactors. Biochem. Eng. J. 32, 33–42. https://doi.org/10.1016/j.bej.2006.08.015.

Chen, C.-Y., Lee, C.-M., Chang, J.-S., 2006b. Feasibility study on bioreactor strategies for enhanced photohydrogen production from *Rhodopseudomonas palustris* WP3-5 using optical-fiber-assisted illumination systems. Int. J. Hydrog. Energy 31, 2345–2355. https://doi.org/10.1016/j.ijhydene.2006.03.007.

Chen, Y.-T., Wu, S.-C., Lee, C.-M., 2012. Relationship between cell growth, hydrogen production and poly-β-hydroxybutyrate (PHB) accumulation by *Rhodopseudomonas palustris* WP3-5. Int. J. Hydrog. Energy 37, 13887–13894. https://doi.org/10.1016/j.ijhydene.2012.06.024.

Chen, G.-Q., Chen, X.-Y., Wu, F.-Q., Chen, J.-C., 2020a. Polyhydroxyalkanoates (PHA) toward cost competitiveness and functionality. Adv. Ind. Eng. Polym. Res. https://doi.org/10.1016/j.aiepr.2019.11.001.

Chen, J., Wei, J., Ma, C., Yang, Z., Li, Z., Yang, X., Wang, M., Zhang, H., Hu, J., Zhang, C., 2020b. Photosynthetic bacteria-based technology is a potential alternative to meet sustainable wastewater treatment requirement? Environ. Int. 137, 105417 https://doi.org/10.1016/j.envint.2019.105417.

Chookaew, T., O-Thong, S., Prasertsan, P., 2015. Biohydrogen production from crude glycerol by two stage of dark and photo fermentation. Int. J. Hydrog. Energy 40, 7433–7438. https://doi.org/10.1016/j.ijhydene.2015.02.133.

Chowdhury, N.B., Alsiyabi, A., Saha, R., 2022. Characterizing the interplay of rubisco and nitrogenase enzymes in anaerobic-photoheterotrophically grown *Rhodopseudomonas palustris* CGA009 through a genome-scale metabolic and expression model. bioRxiv. https://doi.org/10.1101/2022.03.03.482919, 2022.03.03.482919-2022.03.03.482919.

Chylinski, K., Le Rhun, A., Charpentier, E., 2013. The tracrRNA and Cas9 families of Type II CRISPR-Cas immunity systems. RNA Biol. 10 https://doi.org/10.4161/rna.24321.

Colica, G., Caparrotta, S., De Philippis, R., 2012. Selective biosorption and recovery of Ruthenium from industrial effluents with *Rhodopseudomonas palustris* strains. Appl. Microbiol. Biotechnol. 95, 381–387. https://doi.org/10.1007/s00253-012-4053-9.

Colzi, I., Troyan, A.N., Perito, B., Casalone, E., Romoli, R., Pieraccini, G., Škalko-Basnet, N., Adessi, A., Rossi, F., Gonnelli, C., Ristori, S., 2015. Antibiotic delivery by liposomes from prokaryotic microorganisms: Similia cum similis works better. Eur. J. Pharm. Biopharm. 94, 411–418. https://doi.org/10.1016/j.ejpb.2015.06.013.

Corneli, E., Adessi, A., Olguín, E.J., Ragaglini, G., García-López, D.A., De Philippis, R., 2017. Biotransformation of water lettuce (*Pistia stratiotes*) to biohydrogen by *Rhodopseudomonas palustris*. J. Appl. Microbiol. 123, 1438–1446. https://doi.org/10.1111/jam.13599.

Craven, J., Sultan, M.A., Sarma, R., Wilson, S., Meeks, N., Kim, D.Y., Hastings, J.T., Bhattacharyya, D., 2019. *Rhodopseudomonas palustris*-based conversion of organic acids to hydrogen using plasmonic nanoparticles and near-infrared light. RSC Adv. 9 https://doi.org/10.1039/c9ra08747h.

Crovadore, J., Xu, S., Chablais, R., Cochard, B., Lukito, D., Calmin, G., Lefort, F., 2017. Metagenome-assembled genome sequence of *Rhodopseudomonas palustris* strain ELI 1980, commercialized as a biostimulant. Genome Announc. 5 https://doi.org/10.1128/genomeA.00221-17 e00221–17.

Díaz, E., Prieto, M.A., 2000. Bacterial promoters triggering biodegradation of aromatic pollutants. Curr. Opin. Biotechnol. 11, 467–475. https://doi.org/10.1016/S0958-1669(00)00126-9.

Dinesh, G., C, S.M, Karthikeyan, R., Mark, M.J., G, K.R, Arpita, B., Arash, K., 2022. Photoferrotrophs produce a PioAB electron conduit for extracellular electron uptake. MBio 10. https://doi.org/10.1128/mBio.02668-19 e02668–19.

Dipasquale, L., Adessi, A., d'Ippolito, G., Rossi, F., Fontana, A., De Philippis, R., 2015. Introducing capnophilic lactic fermentation in a combined dark-photo fermentation process: a route to unparalleled H_2 yields. Appl. Microbiol. Biotechnol. 99, 1001–1010. https://doi.org/10.1007/s00253-014-6231-4.

Dong, Y., Li, L., Hu, X., Wu, C., 2017. Optimization of o-chlorophenol biodegradation by combined mycelial pellets using response surface methodology. Water Air Soil Pollut. 228, 431. https://doi.org/10.1007/s11270-017-3606-z.

Doud, D.F.R., Angenent, L.T., 2014. Toward electrosynthesis with uncoupled extracellular electron uptake and metabolic growth: enhancing current uptake with *Rhodopseudomonas palustris*. Environ. Sci. Technol. Lett. 1, 351–355. https://doi.org/10.1021/ez500244n.

Doud, D.F.R., Angenent, L.T., 2016. Single-genotype syntrophy by *Rhodopseudomonas palustris* is not a strategy to aid redox balance during anaerobic degradation of lignin monomers. Front. Microbiol. 7, 1082.

Doud, D.F.R., Holmes, E.C., Richter, H., Molitor, B., Jander, G., Angenent, L.T., 2017. Metabolic engineering of *Rhodopseudomonas palustris* for the obligate reduction of n-butyrate to n-butanol. Biotechnol. Biofuels 10, 178. https://doi.org/10.1186/s13068-017-0864-3.

du Toit, J.-P., Pott, R.W.M., 2021. Heat-acclimatised strains of *Rhodopseudomonas palustris* reveal higher temperature optima with concomitantly enhanced biohydrogen production rates. Int. J. Hydrog. Energy 46, 11564–11572. https://doi.org/10.1016/j.ijhydene.2021.01.068.

du Toit, J.-P., Lea-Smith, D.J., Git, A., Hervey, J.R.D., Howe, C.J., Pott, R.W.M., 2021. Expression of alternative nitrogenases in *Rhodopseudomonas palustris* is enhanced using an optimized genetic toolset for rapid, markerless modifications. ACS Synth. Biol. 10, 2167–2178. https://doi.org/10.1021/acssynbio.0c00496.

Egland, P.G., Gibson, J., Harwood, C.S., 1995. Benzoate-coenzyme A ligase, encoded by badA, is one of three ligases able to catalyze benzoyl-coenzyme A formation during anaerobic growth of *Rhodopseudomonas palustris* on benzoate. J. Bacteriol. 177, 6545–6551. https://doi.org/10.1128/jb.177.22.6545-6551.1995.

Egland, P.G., Gibson, J., Harwood, C.S., 2001. Reductive, coenzyme A-mediated pathway for 3-chlorobenzoate degradation in the phototrophic bacterium *Rhodopseudomonas palustris*. Appl. Environ. Microbiol. 67, 1396–1399. https://doi.org/10.1128/AEM.67.3.1396-1399.2001.

Elder, D.J., Morgan, P., Kelly, D.J., 1992. Anaerobic degradation of trans-cinnamate and omega-phenylalkane carboxylic acids by the photosynthetic bacterium *Rhodopseudomonas palustris*: evidence for a beta-oxidation mechanism. Arch. Microbiol. 157, 148–154. https://doi.org/10.1007/BF00245283.

Evans, K., Georgiou, T., Hillon, T., Fordham-Skelton, A., Papiz, M., 2009. Bacteriophytochromes control photosynthesis in *Rhodopseudomonas palustris*. In: Hunter, C.N., Daldal, F., Thurnauer, M.C., Beatty, J.T. (Eds.), The Purple Phototrophic Bacteria. Advances in Photosynthesis and Respiration, Springer, Dordrecht.

Fiβler, J., Kohring, G.W., Giffhorn, F., 1995. Enhanced hydrogen production from aromatic acids by immobilized cells of *Rhodopseudomonas palustris*. Appl. Microbiol. Biotechnol. 44, 43–46. https://doi.org/10.1007/BF00164478.

Gao, R., Wang, Y., Zhang, Y., Tong, J., Dai, W., 2017. Cobalt(II) bioaccumulation and distribution in *Rhodopseudomonas palustris*. Biotechnol. Biotechnol. Equip. 31, 527–534. https://doi.org/10.1080/13102818.2017.1292148.

Geyer, R., Jambeck, J.R., Law, K.L., 2017. Production, use, and fate of all plastics ever made. Sci. Adv. 3, e1700782. https://doi.org/10.1126/sciadv.1700782.

Ghosh, D., Sobro, I.F., Hallenbeck, P.C., 2012. Stoichiometric conversion of biodiesel derived crude glycerol to hydrogen: Response surface methodology study of the effects of light intensity and crude glycerol and glutamate concentration. Bioresour. Technol. 106, 154–160. https://doi.org/10.1016/j.biortech.2011.12.021.

Gifuni, I., Pollio, A., Safi, C., Marzocchella, A., Olivieri, G., 2019. Current bottlenecks and challenges of the microalgal biorefinery. Trends Biotechnol. 37, 242–252. https://doi.org/10.1016/j.tibtech.2018.09.006.

Gosse, J.L., Engel, B.J., Hui, J.C.-H., Harwood, C.S., Flickinger, M.C., 2010. Progress toward a biomimetic leaf: 4,000 h of hydrogen production by coating-stabilized nongrowing photosynthetic *Rhodopseudomonas palustris*. Biotechnol. Prog. 26, 907–918. https://doi.org/10.1002/btpr.406.

Grant, C.R., Komeili, A., 2020. Ferrosomes are iron storage organelles formed by broadly conserved gene clusters in bacteria and archaea. bioRxiv. https://doi.org/10.1101/2020.01.10.902569, 2020.01.10.902569-2020.01.10.902569.

Guardia, A.E., Beligni, M.V., Cortéz, N., Busalmen, J.P., 2020. Electrochemistry of *R. palustris* Azul during phototrophic growth. Electrochim. Acta 355, 136757. https://doi.org/10.1016/j.electacta.2020.136757.

Guzman, M.S., Rengasamy, K., Binkley, M.M., Jones, C., Ranaivoarisoa, T.O., Singh, R., Fike, D.A., Meacham, J.M., Bose, A., 2019. Phototrophic extracellular electron uptake is linked to carbon dioxide fixation in the bacterium *Rhodopseudomonas palustris*. Nat. Commun. https://doi.org/10.1038/s41467-019-09377-6.

Hajighasemi, M., Nocek, B.P., Tchigvintsev, A., Brown, G., Flick, R., Xu, X., Cui, H., Hai, T., Joachimiak, A., Golyshin, P.N., Savchenko, A., Edwards, E.A., Yakunin, A.F., 2016. Biochemical and structural insights into enzymatic depolymerization of polylactic acid and other polyesters by microbial carboxylesterases. Biomacromolecules 17, 2027–2039. https://doi.org/10.1021/acs.biomac.6b00223.

Han, W., Yan, Y., Shi, Y., Gu, J., Tang, J., Zhao, H., 2016. Biohydrogen production from enzymatic hydrolysis of food waste in batch and continuous systems. Sci. Rep. 6 https://doi.org/10.1038/srep38395.

Haq, I.U., Fixen, K.R., 2021. Complete genome sequence of *Rhodopseudomonas palustris* RCB100, an anoxygenic phototroph that degrades 3-chlorobenzoate. Microbiol. Resour. Announc. 10 https://doi.org/10.1128/MRA.00043-21 e00043–21.

Harayama, S., Kishira, H., Kasai, Y., Shutsubo, K., 1999. Petroleum biodegradation in marine environments. J. Mol. Microbiol. Biotechnol. 1, 63–70.

Harwood, C.S., 2022. Rhodopseudomonas palustris. Trends Microbiol. 30, 307–308. https://doi.org/10.1016/j.tim.2021.12.001.

Harwood, C.S., Gibson, J., 1988. Anaerobic and aerobic metabolism of diverse aromatic compounds by the photosynthetic bacterium *Rhodopseudomonas palustris*. Appl. Environ. Microbiol. https://doi.org/10.1128/aem.54.3.712-717.1988.

Heiniger, E.K., Oda, Y., Samanta, S.K., Harwood, C.S., 2012. How posttranslational modification of nitrogenase is circumvented in *Rhodopseudomonas palustris* strains that produce hydrogen gas constitutively. Appl. Environ. Microbiol. 78, 1023–1032. https://doi.org/10.1128/AEM.07254-11.

Hidetada, H., L., S.A, Peter, G.E., S., H.C, 2012a. Anaerobic *p*-coumarate degradation by *Rhodopseudomonas palustris* and identification of CouR, a MarR repressor protein that binds *p*-coumaroyl coenzyme A. J. Bacteriol. 194, 1960–1967. https://doi.org/10.1128/JB.06817-11.

Hidetada, H., S., H.C., B., P.K., L., S.A, Peter, G.E., 2012b. Antisense RNA that affects *Rhodopseudomonas palustris* quorum-sensing signal receptor expression. Proc. Natl. Acad. Sci. 109, 12141–12146. https://doi.org/10.1073/pnas.1200243109.

Hirakawa, H., Hirakawa, Y., Greenberg, E.P., Harwood, C.S., 2015. BadR and BadM proteins transcriptionally regulate two operons needed for anaerobic benzoate degradation by *Rhodopseudomonas palustris*. Appl. Environ. Microbiol. 81, 4253–4262. https://doi.org/10.1128/AEM.00377-15.

Hitit, Z.Y., Lazaro, C.Z., Hallenbeck, P.C., 2017a. Single stage hydrogen production from cellulose through photo-fermentation by a co-culture of *Cellulomonas fimi* and *Rhodopseudomonas palustris*. Int. J. Hydrog. Energy 42, 6556–6566. https://doi.org/10.1016/j.ijhydene.2016.12.035.

Hitit, Z.Y., Lazaro, C.Z., Hallenbeck, P.C., 2017b. Hydrogen production by co-cultures of *Clostridium butyricum* and *Rhodospeudomonas palustris*: Optimization of yield using response surface methodology. Int. J. Hydrog. Energy 42, 6578–6589. https://doi.org/10.1016/j.ijhydene.2016.12.122.

Hitit, Z.Y., Zampol Lazaro, C., Hallenbeck, P.C., 2017c. Increased hydrogen yield and COD removal from starch/glucose based medium by sequential dark and photo-fermentation using *Clostridium butyricum* and *Rhodopseudomonas palustris*. Int. J. Hydrog. Energy 42, 18832–18843. https://doi.org/10.1016/j.ijhydene.2017.05.161.

Hosseini, S.S., Aghbashlo, M., Tabatabaei, M., Najafpour, G., Younesi, H., 2015. Thermodynamic evaluation of a photobioreactor for hydrogen production from syngas via a locally isolated *Rhodopseudomonas palustris* PT. Int. J. Hydrog. Energy 40, 14246–14256. https://doi.org/10.1016/j.ijhydene.2015.08.092.

Howe, C.J., Bombelli, P., 2020. Electricity production by photosynthetic microorganisms. Joule 4, 2065–2069. https://doi.org/10.1016/j.joule.2020.09.003.

Hsu, S.-H., Shen, M.-W., Chen, J.-C., Lur, H.-S., Liu, C.-T., 2021. The photosynthetic bacterium *Rhodopseudomonas palustris* strain PS3 exerts plant growth-promoting effects by stimulating nitrogen uptake and elevating auxin levels in expanding leaves. Front. Plant Sci. 12, 93.

Hu, C.-W., Lin, M.-H., Huang, H.-C., Ku, W.-C., Yi, T.-H., Tsai, C.-F., Chen, Y.-J., Sugiyama, N., Ishihama, Y., Juan, H.-F., Wu, S.-H., 2012. Phosphoproteomic analysis of *Rhodopseudomonas palustris* reveals the role of pyruvate phosphate dikinase phosphorylation in lipid production. J. Proteome Res. 11, 5362–5375. https://doi.org/10.1021/pr300582p.

Hu, C., Choy, S.-Y., Giannis, A., 2018. Evaluation of lighting systems, carbon sources, and bacteria cultures on photofermentative hydrogen production. Appl. Biochem. Biotechnol. 185, 257–269. https://doi.org/10.1007/s12010-017-2655-5.

Huang, J.J., Heiniger, E.K., McKinlay, J.B., Harwood, C.S., 2010. Production of hydrogen gas from light and the inorganic electron donor thiosulfate by *Rhodopseudomonas palustris*. Appl. Environ. Microbiol. 76, 7717–7722. https://doi.org/10.1128/AEM.01143-10.

Ibrahim, M., Raajaraam, L., Raman, K., 2021. Modelling microbial communities: Harnessing consortia for biotechnological applications. Comput. Struct. Biotechnol. J. 19, 3892–3907. https://doi.org/10.1016/j.csbj.2021.06.048.

Immethun, C.M., Kathol, M., Changa, T., Saha, R., 2022. Synthetic biology tool development advances predictable gene expression in the metabolically versatile soil bacterium *Rhodopseudomonas palustris*. Front. Bioeng. Biotechnol. 318.

Inglesby, A., Beatty, D., Fisher, A., 2012. *Rhodopseudomonas palustris* purple bacteria fed *Arthrospira maxima* cyanobacteria: Demonstration of application in microbial fuel cells. RSC Adv. 2, 4829–4838. https://doi.org/10.1039/C2RA20264F.

Inui, M., Roh, J.H., Zahn, K., Yukawa, H., 2000. Sequence analysis of the cryptic plasmid pMG101 from *Rhodopseudomonas palustris* and construction of stable cloning vectors. Appl. Environ. Microbiol. 66, 54–63. https://doi.org/10.1128/AEM.66.1.54-63.2000.

Jackson, P.J., Hitchcock, A., Swainsbury, D.J.K., Qian, P., Martin, E.C., Farmer, D.A., Dickman, M.J., Canniffe, D.P., Hunter, C.N., 2018. Identification of protein W, the elusive sixth subunit of the *Rhodopseudomonas palustris* reaction center-light harvesting 1 core complex. Biochim. Biophys. Acta Bioenerg. 1859, 119–128. https://doi.org/10.1016/J.BBABIO.2017.11.001.

Jadhav, D.A., Mungray, A.K., Arkatkar, A., Kumar, S.S., 2021. Recent advancement in scaling-up applications of microbial fuel cells: From reality to practicability. Sustain. Energy Technol. Assess. https://doi.org/10.1016/j.seta.2021.101226.

Jamil, Z., Mohamad Annuar, M.S., Ibrahim, S., Vikineswary, S., 2009. Optimization of phototrophic hydrogen production by *Rhodopseudomonas palustris* PBUM001 via statistical experimental design. Int. J. Hydrog. Energy 34, 7502–7512. https://doi.org/10.1016/j.ijhydene.2009.05.116.

Joshi, G.S., Romagnoli, S., Verberkmoes, N.C., Hettich, R.L., Pelletier, D., Tabita, F.R., 2009. Differential accumulation of form I RubisCO in *Rhodopseudomonas palustris* CGA010 under photoheterotrophic growth conditions with reduced carbon sources. J. Bacteriol. 191, 4243–4250. https://doi.org/10.1128/JB.01795-08.

Kamal, V.S., Wyndham, R.C., 1990. Anaerobic phototrophic metabolism of 3-chlorobenzoate by *Rhodopseudomonas palustris* WS17. Appl. Environ. Microbiol. 56, 3871–3873. https://doi.org/10.1128/aem.56.12.3871-3873.1990.

Kantachote, D., Nunkaew, T., Kantha, T., Chaiprapat, S., 2016. Biofertilizers from *Rhodopseudomonas palustris* strains to enhance rice yields and reduce methane emissions. Appl. Soil Ecol. 100, 154–161. https://doi.org/10.1016/j.apsoil.2015.12.015.

Kantha, T., Kantachote, D., Klongdee, N., 2015. Potential of biofertilizers from selected *Rhodopseudomonas palustris* strains to assist rice (*Oryza sativa* L. subsp. *indica*) growth under salt stress and to reduce greenhouse gas emissions. Ann. Microbiol. 65, 2109–2118. https://doi.org/10.1007/s13213-015-1049-6.

Kanwal, F., Tahir, A., Qadir Shah, S.A., Tsuzuki, T., Nisbet, D., Chen, J., Rehman, Y., 2020. Effect of phyto-fabricated nanoscale organic-iron complex on photo-fermentative hydrogen production by *Rhodopseudomonas palustris* MP2 and *Rhodopseudomonas palustris* MP4. Biomass Bioenergy 140, 105667. https://doi.org/10.1016/j.biombioe.2020.105667.

Kernan, C., Chow, P.P., Christianson, R.J., Huang, J., 2015. Experimental and computational investigation of biofilm formation by *Rhodopseudomonas palustris* growth under two metabolic modes. PLoS One 10. https://doi.org/10.1371/journal.pone.0129354 e0129354–e0129354.

Kim, J.K., Lee, B.-K., 2000. Mass production of *Rhodopseudomonas palustris* as diet for aquaculture. Aquac. Eng. 23, 281–293. https://doi.org/10.1016/S0144-8609(00)00057-1.

Kim, M.K., Choi, K.-M., Yin, C.-R., Lee, K.-Y., Im, W.-T., Lim, J.H., Lee, S.-T., 2004. Odorous swine wastewater treatment by purple non-sulfur bacteria, *Rhodopseudomonas palustris*, isolated from eutrophicated ponds. Biotechnol. Lett. 26, 819–822. https://doi.org/10.1023/b:bile.0000025884.50198.67.

Kour, D., Rana, K.L., Yadav, N., Yadav, A.N., Rastegari, A., Singh, Negi, D.P., Singh, K., Saxena, A., 2019. Technologies for Biofuel Production: Current Development, Challenges, and Future Prospects, pp. 1–50. https://doi.org/10.1007/978-3-030-14463-0_1.

Larimer, F.W., Chain, P., Hauser, L., Lamerdin, J., Malfatti, S., Do, L., Land, M.L., Pelletier, D.A., Beatty, J.T., Lang, A.S., Tabita, F.R., Gibson, J.L., Hanson, T.E., Bobst, C., Torres, Y., Torres, J.L., Peres, C., Harrison, F.H., Gibson, J., Harwood, C.S., 2004. Complete genome sequence of the metabolically versatile photosynthetic bacterium *Rhodopseudomonas palustris*. Nat. Biotechnol. https://doi.org/10.1038/nbt923.

Lee, C.-M., Yu, K.-M., Chen, P.-C., 2006. Limiting factors of photo-hydrogen production by *Rhodopseudomonas palustris* WP3–5. Mod. Multidiscip. Appl. Microbiol. https://doi.org/10.1002/9783527611904.ch40.

Lee, C.-M., Hung, G.-J., Yang, C.-F., 2011. Hydrogen production by *Rhodopseudomonas palustris* WP 3-5 in a serial photobioreactor fed with hydrogen fermentation effluent. Bioresour. Technol. 102, 8350–8356. https://doi.org/10.1016/j.biortech.2011.04.072.

Lee, S., Kang, M., Bae, J.-H., Sohn, J.-H., Sung, B.H., 2019. Bacterial valorization of lignin: strains, enzymes, conversion pathways, biosensors, and perspectives. Front. Bioeng. Biotechnol. 7, 209. https://doi.org/10.3389/fbioe.2019.00209.

Levin, D.B., Pitt, L., Love, M., 2004. Biohydrogen production: prospects and limitations to practical application. Int. J. Hydrog. Energy 29, 173–185. https://doi.org/10.1016/S0360-3199(03)00094-6.

Li, Y.-J., Wang, R., Lin, C.-Y., Chen, S.-H., Chuang, C.-H., Chou, T.-H., Ko, C.-F., Chou, P.-H., Liu, C.-T., Shih, Y., 2021. The degradation mechanisms of *Rhodopseudomonas palustris* toward hexabromocyclododecane by time-course transcriptome analysis. Chem. Eng. J. 425, 130489 https://doi.org/10.1016/j.cej.2021.130489.

Liao, Q., Zhong, N.-B., Zhu, X., Chen, R., Wang, Y.-Z., Lee, D.-J., 2013. Enhancement of hydrogen production by adsorption of *Rhodoseudomonas palustris* CQK 01 on a new support material. Int. J. Hydrog. Energy 38, 15730–15737. https://doi.org/10.1016/j.ijhydene.2013.04.146.

Liu, G., Zhou, J., Wang, J., Song, Z., Qv, Y., 2006. Bacterial decolorization of azo dyes by *Rhodopseudomonas palustris*. World J. Microbiol. Biotechnol. 22, 1069–1074. https://doi.org/10.1007/s11274-005-4857-1.

Liu, Y., Ghosh, D., Hallenbeck, P.C., 2015. Biological reformation of ethanol to hydrogen by *Rhodopseudomonas palustris* CGA009. Bioresour. Technol. 176, 189–195. https://doi.org/10.1016/j.biortech.2014.11.047.

Liu, C.-H., Lee, S.-K., Ou, I.-C., Tsai, K.-J., Lee, Y., Chu, Y.-H., Liao, Y.-T., Liu, C.-T., 2021. Essential factors that affect bioelectricity generation by *Rhodopseudomonas palustris* strain PS3 in paddy soil microbial fuel cells. Int. J. Energy Res. 45, 2231–2244. https://doi.org/10.1002/er.5916.

Llorens, I., Untereiner, G., Jaillard, D., Gouget, B., Chapon, V., Carriere, M., 2012. Uranium interaction with two multi-resistant environmental bacteria: *Cupriavidus metallidurans* CH34 and *Rhodopseudomonas palustris*. PLoS One 7, e51783.

Lo, Y.-C., Chen, C.-Y., Lee, C.-M., Chang, J.-S., 2010. Sequential dark-photo fermentation and autotrophic microalgal growth for high-yield and CO. Int. J. Hydrog. Energy 35, 10944–10953. https://doi.org/10.1016/j.ijhydene.2010.07.090.

Lo, K.-J., Lee, S.-K., Liu, C.-T., 2020. Development of a low-cost culture medium for the rapid production of plant growth-promoting *Rhodopseudomonas palustris* strain PS3. PLoS One 15 e0236739–e0236739.

Luo, X., Zhang, D., Zhou, X., Du, J., Zhang, S., Liu, Y., 2018. Cloning and characterization of a pyrethroid pesticide decomposing esterase gene, *Est3385*, from *Rhodopseudomonas palustris* PSB-S. Sci. Rep. 8, 7384. https://doi.org/10.1038/s41598-018-25734-9.

Luo, L., Wang, P., Zhai, Z., Su, P., Tan, X., Zhang, D., Zhang, Z., Liu, Y., 2019. The effects of *Rhodopseudomonas palustris* PSB06 and CGA009 with different agricultural applications on rice growth and rhizosphere bacterial communities. AMB Express 9, 173. https://doi.org/10.1186/s13568-019-0897-z.

Ma, E., Harrington, L.B., O'Connell, M.R., Zhou, K., Doudna, J.A., 2015. Single-stranded DNA cleavage by divergent CRISPR-Cas9 enzymes. Mol. Cell 60. https://doi.org/10.1016/j.molcel.2015.10.030.

Ma, Y., Donohue, T.J., Noguera, D.R., 2021. Kinetic modeling of anaerobic degradation of plant-derived aromatic mixtures by *Rhodopseudomonas palustris*. Biodegradation 32, 179–192. https://doi.org/10.1007/s10532-021-09932-3.

Mabutyana, L., Pott, R.W.M., 2021. Photo-fermentative hydrogen production by *Rhodopseudomonas palustris* CGA009 in the presence of inhibitory compounds. Int. J. Hydrog. Energy. https://doi.org/10.1016/j.ijhydene.2020.12.189.

McCormick, A.J., Bombelli, P., Bradley, R.W., Thorne, R., Wenzel, T., Howe, C.J., 2015. Biophotovoltaics: oxygenic photosynthetic organisms in the world of bioelectrochemical systems. Energy Environ. Sci. 8, 1092–1109. https://doi.org/10.1039/C4EE03875D.

McCully, A., McKinlay, J., 2016. Disrupting Calvin cycle phosphoribulokinase activity in *Rhodopseudomonas palustris* increases the H_2 yield and specific production rate proportionately. Int. J. Hydrog. Energy 41. https://doi.org/10.1016/j.ijhydene.2016.01.003.

McKinlay, J.B., Oda, Y., Ruhl, M., Posto, A.L., Sauer, U., Harwood, C.S., 2014. Non-growing *Rhodopseudomonas palustris* increases the hydrogen gas yield from acetate by shifting from the glyoxylate shunt to the tricarboxylic acid cycle. J. Biol. Chem. https://doi.org/10.1074/jbc.M113.527515.

Morishima, K., Yoshida, M., Furuya, A., Moriuchi, T., Ota, M., Furukawa, Y., 2007. Improving the performance of a direct photosynthetic/metabolic bio-fuel cell (DPBFC) using gene manipulated bacteria. J. Micromech. Microeng. 17, S274–S279. https://doi.org/10.1088/0960-1317/17/9/s10.

Mouhib, M., Antonucci, A., Reggente, M., Amirjani, A., Gillen, A.J., Boghossian, A.A., 2019. Enhancing bioelectricity generation in microbial fuel cells and biophotovoltaics using nanomaterials. Nano Res. 12, 2184–2199. https://doi.org/10.1007/s12274-019-2438-0.

Mutharasaiah, K., Govindareddy, V., Chandrakant, K., 2012. Biodegradation of 2-chlorophenol by *Rhodopseudomonas palustris*. Bioremediat. J. 16, 1–8. https://doi.org/10.1080/10889868.2011.628348.

Muzziotti, D., Adessi, A., Faraloni, C., Torzillo, G., De Philippis, R., 2017. Acclimation strategy of *Rhodopseudomonas palustris* to high light irradiance. Microbiol. Res. https://doi.org/10.1016/j.micres.2017.01.007.

Nagadomi, H., Kitamura, T., Watanabe, M., Sasaki, K., 2000. Simultaneous removal of chemical oxygen demand (COD), phosphate, nitrate and H_2S in the synthetic sewage wastewater using porous ceramic immobilized photosynthetic bacteria. Biotechnol. Lett. 22, 1369–1374. https://doi.org/10.1023/A:1005688229783.

Navid, A., Jiao, Y., Wong, S.E., Pett-Ridge, J., 2019. System-level analysis of metabolic trade-offs during anaerobic photoheterotrophic growth in *Rhodopseudomonas palustris*. BMC Bioinform. 20, 233. https://doi.org/10.1186/s12859-019-2844-z.

Neubauer, C., Dalleska, N.F., Cowley, E.S., Shikuma, N.J., Wu, C.-H., Sessions, A.L., Newman, D.K., 2015. Lipid remodeling in *Rhodopseudomonas palustris* TIE-1 upon loss of hopanoids and hopanoid methylation. Geobiology 13, 443–453. https://doi.org/10.1111/gbi.12143.

Oda, Y., Samanta, S.K., Rey, F.E., Wu, L., Liu, X., Yan, T., Zhou, J., Harwood, C.S., 2005. Functional genomic analysis of three nitrogenase isozymes in the photosynthetic bacterium *Rhodopseudomonas palustris*. J. Bacteriol. 187, 7784–7794. https://doi.org/10.1128/JB.187.22.7784-7794.2005.

Oh, Y.-K., Seol, E.-H., Lee, E.Y., Park, S., 2002. Fermentative hydrogen production by a new chemoheterotrophic bacterium *Rhodopseudomonas palustris* P4. Int. J. Hydrog. Energy 27, 1373–1379. https://doi.org/10.1016/S0360-3199(02)00100-3.

Oh, Y.-K., Seol, E.-H., Kim, M.-S., Park, S., 2004. Photoproduction of hydrogen from acetate by a chemoheterotrophic bacterium *Rhodopseudomonas palustris* P4. Int. J. Hydrog. Energy 29, 1115–1121. https://doi.org/10.1016/j.ijhydene.2003.11.008.

Oh, Y.-K., Kim, Y.-J., Park, J.-Y., Lee, T.H., Kim, M.-S., Park, S., 2005. Biohydrogen production from carbon monoxide and water by *Rhodopseudomonas palustris* P4. Biotechnol. Bioprocess Eng. 10, 270. https://doi.org/10.1007/BF02932024.

Oshlag, J.Z., Ma, Y., Morse, K., Burger, B.T., Lemke, R.A., Karlen, S.D., Myers, K.S., Donohue, T.J., Noguera, D.R., 2020. Anaerobic degradation of syringic acid by an adapted strain of *Rhodopseudomonas palustris*. Appl. Environ. Microbiol. 86 https://doi.org/10.1128/AEM.01888-19 e01888–19.

Otani, S., Nguyen, D.-T., Taguchi, K., 2020. Enhancing the power generation of *Rhodopseudomonas palustris*-based MFC. Int. J. Appl. Electromagn. Mech. 64, 1261–1268. https://doi.org/10.3233/JAE-209444.

Padovani, G., Vaičiulytė, S., Carlozzi, P., 2016. BioH_2 photoproduction by means of *Rhodopseudomonas palustris* sp. cultured in a lab-scale photobioreactor operated in batch, fed-batch and semi-continuous modes. Fuel 166, 203–210. https://doi.org/10.1016/j.fuel.2015.10.124.

Padovani, G., Emiliani, G., Giovanelli, A., Traversi, M.L., Carlozzi, P., 2018. Assessment of glycerol usage by five different purple non-sulfur bacterial strains for bioplastic production. J. Environ. Chem. Eng. 6, 616–622. https://doi.org/10.1016/j.jece.2017.12.050.

Pan, C., Oda, Y., Lankford, P.K., Zhang, B., Samatova, N.F., Pelletier, D.A., Harwood, C.S., Hettich, R.L., 2008. Characterization of anaerobic catabolism of *p*-coumarate in *Rhodopseudomonas palustris* by integrating transcriptomics and quantitative proteomics. Cell. Proteomics 7. https://doi.org/10.1074/mcp.M700147-MCP200, 938 LP – 948.

Pandey, Ashutosh, Pandey, Archana, Srivastava, P., Pandey, Anjana, 2007. Using reverse micelles as microreactor for hydrogen production by coupled systems of *Nostoc/R. palustris* and *Anabaena/R. palustris*. World J. Microbiol. Biotechnol. 23, 269–274. https://doi.org/10.1007/s11274-006-9224-3.

Pandit, S., Savla, N., Jung, S.P., 2020. Recent advancements in scaling up microbial fuel cells. In: Abbassi, R., Yadav, A.K., Khan, F., Garaniya, V. (Eds.), Integrated Microbial Fuel Cells for Wastewater Treatment. https://doi.org/10.1016/B978-0-12-817493-7.00016-3.

Pankan, A.O., Yunus, K., Fisher, A.C., 2020. Mechanistic evaluation of the exoelectrogenic activity of *Rhodopseudomonas palustris* under different nitrogen regimes. Bioresour. Technol. 300, 122637 https://doi.org/10.1016/j.biortech.2019.122637.

Park, T.-J., Ding, W., Cheng, S., Brar, M.S., Ma, A.P.Y., Tun, H.M., Leung, F.C., 2014. Microbial community in microbial fuel cell (MFC) medium and effluent enriched with purple photosynthetic bacterium (*Rhodopseudomonas* sp.). AMB Express 4, 22. https://doi.org/10.1186/s13568-014-0022-2.

Pechter, K.B., Gallagher, L., Pyles, H., Manoil, C.S., Harwood, C.S., 2015. Essential genome of the metabolically versatile alphaproteobacterium *Rhodopseudomonas palustris*. J. Bacteriol. 198, 867–876. https://doi.org/10.1128/JB.00771-15.

Phongjarus, N., Suvaphat, C., Srichai, N., Ritchie, R.J., 2018. Photoheterotrophy of photosynthetic bacteria (*Rhodopseudomonas palustris*) growing on oil palm and soybean cooking oils. Environ. Technol. Innov. https://doi.org/10.1016/j.eti.2018.03.002.

Pintucci, C., Giovannelli, A., Traversi, M.L., Ena, A., Padovani, G., Carlozzi, P., 2013. Fresh olive mill waste deprived of polyphenols as feedstock for hydrogen photo-production by means of *Rhodopseudomonas palustris* 42OL. Renew. Energy 51, 358–363. https://doi.org/10.1016/j.renene.2012.09.037.

Pintucci, C., Padovani, G., Giovannelli, A., Traversi, M.L., Ena, A., Pushparaj, B., Carlozzi, P., 2015. Hydrogen photo-evolution by *Rhodopseudomonas palustris* 6A using pre-treated olive mill wastewater and a synthetic medium containing sugars. Energy Convers. Manag. 90, 499–505. https://doi.org/10.1016/j.enconman.2014.11.045.

Piskorska, M., Soule, T., Gosse, J.L., Milliken, C., Flickinger, M.C., Smith, G.W., Yeager, C.M., 2013. Preservation of H_2 production activity in nanoporous latex coatings of *Rhodopseudomonas palustris* CGA009 during dry storage at ambient temperatures. Microb. Biotechnol. 6, 515–525. https://doi.org/10.1111/1751-7915.12032.

Ponnusamy, V.K., Nguyen, D.D., Dharmaraja, J., Shobana, S., Banu, J.R., Saratale, R.G., Chang, S.W., Kumar, G., 2019. A review on lignin structure, pretreatments, fermentation reactions and biorefinery potential. Bioresour. Technol. 271, 462–472. https://doi.org/10.1016/j.biortech.2018.09.070.

Pott, R.W.M., Howe, C.J., Dennis, J.S., 2014. The purification of crude glycerol derived from biodiesel manufacture and its use as a substrate by *Rhodopseudomonas palustris* to produce hydrogen. Bioresour. Technol. 152, 464–470. https://doi.org/10.1016/j.biortech.2013.10.094.

Qi, X., Ren, Y., Wang, X., 2017. New advances in the biodegradation of poly(lactic) acid. Int. Biodeterior. Biodegradation 117, 215–223. https://doi.org/10.1016/j.ibiod.2017.01.010.

Qi, X., Bo, Y., Ren, Y., Wang, X., 2018a. The anaerobic biodegradation of poly(lactic) acid textiles in photosynthetic microbial fuel cells: Self-sustained bioelectricity generation. Polym. Degrad. Stab. 148, 42–49. https://doi.org/10.1016/j.polymdegradstab. 2018.01.005.

Qi, X., Tian, E., Ren, Y., Wang, X., 2018b. A weak infrared light strengthens anoxygenic photosynthetic bacteria activated sludge for the anaerobic biodegradation of polylactic acid in microbial fuel cell systems. Polym. Degrad. Stab. 157, 44–52. https://doi.org/10.1016/j.polymdegradstab. 2018.09.024.

Qian, E.W., 2013. Pretreatment and saccharification of lignocellulosic biomass. In: Tojo, S., Hirasawa, T. (Eds.), Research Approaches to Sustainable Biomass Systems. https://doi.org/10.1016/B978-0-12-404609-2.00007-6.

Qin, L., Liu, Q., Meng, Q., Fan, Z., He, J., Liu, T., Shen, C., Zhang, G., 2017. Anoxic oscillating MBR for photosynthetic bacteria harvesting and high salinity wastewater treatment. Bioresour. Technol. 224, 69–77. https://doi.org/10.1016/j.biortech.2016.10.067.

Rahalkar, S.B., Joshi, S.R., Shivaraman, N., 1993. Photometabolism of aromatic compounds by *Rhodopseudomonas palustris*. Curr. Microbiol. 26, 1–9. https://doi.org/10.1007/BF01577235.

Ranaivoarisoa, T.O., Singh, R., Rengasamy, K., Guzman, M.S., Bose, A., 2019. Towards sustainable bioplastic production using the photoautotrophic bacterium *Rhodopseudomonas palustris* TIE-1. J. Ind. Microbiol. Biotechnol. https://doi.org/10.1007/s10295-019-02165-7.

Rayyan, A., Meyer, T., Kyndt, J., 2018. Draft whole-genome sequence of the purple photosynthetic bacterium *Rhodopseudomonas palustris* XCP. Microbiol. Resour. Announc. 7 https://doi.org/10.1128/MRA.00855-18 e00855–18.

Rengasamy, K., Ranaivoarisoa, T., Singh, R., Bose, A., 2018. An insoluble iron complex coated cathode enhances direct electron uptake by *Rhodopseudomonas palustris* TIE-1. Bioelectrochemistry 122, 164–173. https://doi.org/10.1016/j.bioelechem.2018.03.015.

Rengasamy, K., Ranaivoarisoa, T., Bai, W., Bose, A., 2020. Magnetite nanoparticle anchored graphene cathode enhances microbial electrosynthesis of polyhydroxybutyrate by *Rhodopseudomonas palustris* TIE-1. Nanotechnology 32, 35103. https://doi.org/10.1088/1361-6528/abbe58.

Rey, F.E., Harwood, C.S., 2010. FixK, a global regulator of microaerobic growth, controls photosynthesis in *Rhodopseudomonas palustris*. Mol. Microbiol. 75, 1007–1020. https://doi.org/10.1111/j.1365-2958.2009.07037.x.

Rey, F.E., Heiniger, E.K., Harwood, C.S., 2007. Redirection of metabolism for biological hydrogen production. Appl. Environ. Microbiol. 73, 1665–1671. https://doi.org/10.1128/AEM.02565-06.

Rhee, S.-K., Liu, X., Wu, L., Chong, S.C., Wan, X., Zhou, J., 2004. Detection of genes involved in biodegradation and biotransformation in microbial communities by using 50-mer oligonucleotide microarrays. Appl. Environ. Microbiol. 70, 4303–4317. https://doi.org/10.1128/AEM.70.7.4303-4317.2004.

Rikame, S.S., Mungray, A.A., Mungray, A.K., 2022. Chapter 16 - Microbial fuel cell: Commercial aspect in terms of stacking and electrochemical perspective for scaling up. In: Jadhav, D.A., Pandit, S., Gajalakshmi, S., Shah, M.P. (Eds.), Scaling Up of Microbial Electrochemical Systems. Elsevier, pp. 291–308. https://doi.org/10.1016/B978-0-323-90765-1.00016-2.

Ross, B.S., Pott, R.W.M., 2021. Hydrogen production by immobilized *Rhodopseudomonas palustris* in packed or fluidized bed photobioreactor systems. Int. J. Hydrog. Energy 46, 1715–1727. https://doi.org/10.1016/j.ijhydene.2020.10.061.

Rouphael, Y., Colla, G., 2020. Editorial: Biostimulants in agriculture. Front. Plant Sci. 11, 4. https://doi.org/10.3389/fpls.2020.00040.

Sabourin-Provost, G., Hallenbeck, P.C., 2009. High yield conversion of a crude glycerol fraction from biodiesel production to hydrogen by photofermentation. Bioresour. Technol. 100, 3513–3517. https://doi.org/10.1016/j.biortech.2009.03.027.

Sakarika, M., Spanoghe, J., Sui, Y., Wambacq, E., Grunert, O., Haesaert, G., Spiller, M., Vlaeminck, S.E., 2020. Purple non-sulphur bacteria and plant production: benefits for fertilization, stress resistance and the environment. Microb. Biotechnol. 13, 1336–1365. https://doi.org/10.1111/1751-7915.13474.

Salmon, R.C., Cliff, M.J., Rafferty, J.B., Kelly, D.J., 2013. The CouPSTU and TarPQM transporters in *Rhodopseudomonas palustris*: redundant, promiscuous uptake systems for lignin-derived aromatic substrates. PLoS One. https://doi.org/10.1371/journal.pone.0059844.

Satagopan, S., Chan, S., Perry, L.J., Tabita, F.R., 2014. Structure-function studies with the unique hexameric form II ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) from *Rhodopseudomonas palustris*. J. Biol. Chem. 289, 21433–21450. https://doi.org/10.1074/jbc.M114.578625.

Saunders, S.H., Tse, E.C.M., Yates, M.D., Otero, F.J., Trammell, S.A., Stemp, E.D.A., Barton, J.K., Tender, L.M., Newman, D.K., 2020. Extracellular DNA promotes efficient extracellular electron transfer by pyocyanin in *Pseudomonas aeruginosa* biofilms. Cell 182. https://doi.org/10.1016/j.cell.2020.07.006.

Schaefer, A.L., Greenberg, E.P., Oliver, C.M., Oda, Y., Huang, J.J., Bittan-Banin, G., Peres, C.M., Schmidt, S., Juhaszova, K., Sufrin, J.R., Harwood, C.S., 2008. A new class of homoserine lactone quorum-sensing signals. Nature 454, 595–599. https://doi.org/10.1038/nature07088.

Sharma, N., Doerner, K.C., Alok, P.C., Choudhary, M., 2015. Skatole remediation potential of *Rhodopseudomonas palustris* WKU-KDNS3 isolated from an animal waste lagoon. Lett. Appl. Microbiol. 60, 298–306. https://doi.org/10.1111/lam.12379.

Sharma, S., Basu, S., Shetti, N.P., Aminabhavi, T.M., 2020. Waste-to-energy nexus for circular economy and environmental protection: Recent trends in hydrogen energy. Sci. Total Environ. 713, 136633 https://doi.org/10.1016/j.scitotenv.2020.136633.

Shi, X.-Y., Li, W.-W., Yu, H.-Q., 2014. Optimization of H_2 photo-fermentation from benzoate by *Rhodopseudomonas palustris* using a desirability function approach. Int. J. Hydrog. Energy 39, 4244–4251. https://doi.org/10.1016/j.ijhydene.2014.01.016.

Singh, A., Sevda, S., Abu Reesh, I.M., Vanbroekhoven, K., Rathore, D., Pant, D., 2015. Biohydrogen production from lignocellulosic biomass: Technology and sustainability. Energies 8. https://doi.org/10.3390/en81112357.

Su, H., Cheng, J., Zhou, J., Song, W., Cen, K., 2009a. Combination of dark- and photo-fermentation to enhance hydrogen production and energy conversion efficiency. Int. J. Hydrog. Energy 34, 8846–8853. https://doi.org/10.1016/j.ijhydene.2009.09.001.

Su, H., Cheng, J., Zhou, J., Song, W., Cen, K., 2009b. Improving hydrogen production from cassava starch by combination of dark and photo fermentation. Int. J. Hydrog. Energy 34, 1780–1786. https://doi.org/10.1016/j.ijhydene.2008.12.045.

Su, P., Tan, X., Li, C., Zhang, D., Cheng, J., Zhang, S., Zhou, X., Yan, Q., Peng, J., Zhang, Z., Liu, Y., Lu, X., 2017. Photosynthetic bacterium *Rhodopseudomonas palustris* GJ-22 induces systemic resistance against viruses. Microb. Biotechnol. 10, 612–624. https://doi.org/10.1111/1751-7915.12704.

Tian, X., Liao, Q., Liu, W., Wang, Y.Z., Zhu, X., Li, J., Wang, H., 2009. Photo-hydrogen production rate of a PVA-boric acid gel granule containing immobilized photosynthetic bacteria cells. Int. J. Hydrog. Energy 34, 4708–4717. https://doi.org/10.1016/j.ijhydene.2009.03.042.

Tian, X., Liao, Q., Zhu, X., Wang, Y., Zhang, P., Li, J., Wang, H., 2010. Characteristics of a biofilm photobioreactor as applied to photo-hydrogen production. Bioresour. Technol. 101, 977–983. https://doi.org/10.1016/j.biortech.2009.09.007.

Tian, Y., Wu, X., Feng, B., Tian, C., Wang, C., Xiao, B., 2017. Nutrient recovery from cyanobacteria biomasses using purple nonsulfur bacterium *Rhodopseudomonas palustris*. Pol. J. Environ. Stud. 26, 2767–2775. https://doi.org/10.15244/pjoes/70403.

Touloupakis, E., Poloniataki, E.G., Ghanotakis, D.F., Carlozzi, P., 2021. Production of biohydrogen and/or poly-β-hydroxybutyrate by *Rhodopseudomonas* sp. using various carbon sources as substrate. Appl. Biochem. Biotechnol. 193, 307–318. https://doi.org/10.1007/s12010-020-03428-1.

Venkidusamy, K., Megharaj, M., 2016. A novel electrophototrophic bacterium *Rhodopseudomonas palustris* strain RP2, exhibits hydrocarbonoclastic potential in anaerobic environments. Front. Microbiol. 85 e02671–18.

Wampler, D.A., Ensign, S.A., 2005. Photoheterotrophic metabolism of acrylamide by a newly isolated strain of *Rhodopseudomonas palustris*. Appl. Environ. Microbiol. 71, 5850–5857. https://doi.org/10.1128/AEM.71.10.5850-5857.2005.

Wang, X., Chen, J., Tang, X., Wang, J., Zhu, L., Zhang, W., Wang, H., Li, Y., Zhang, Q., 2019c. Biodegradation mechanism of polyesters by hydrolase from *Rhodopseudomonas palustris*: an *in silico* approach. Chemosphere 231, 126–133. https://doi.org/10.1016/j.chemosphere.2019.05.112.

Wang, X., Cheng, X., Sun, D., Qi, H., 2008. Biodecolorization and partial mineralization of Reactive Black 5 by a strain of *Rhodopseudomonas palustris*. J. Environ. Sci. 20, 1218–1225. https://doi.org/10.1016/S1001-0742(08)62212-3.

Wang, X., Feng, Y., Wang, H., Qu, Y., Yu, Y., Ren, N., Li, N., Wang, E., Lee, H., Logan, B. E., 2009. Bioaugmentation for electricity generation from corn stover biomass using microbial fuel cells. Environ. Sci. Technol. 43, 6088–6093. https://doi.org/10.1021/es900391b.

Wang, Y.-Z., Xie, X.-W., Zhu, X., Liao, Q., Chen, R., Zhao, X., Lee, D.-J., 2012. Hydrogen production by *Rhodopseudomonas palustris* CQK 01 in a continuous photobioreactor with ultrasonic treatment. Int. J. Hydrog. Energy 37, 15450–15457. https://doi.org/10.1016/j.ijhydene.2012.02.187.

Wang, Y.-Z., Liao, Q., Zhu, X., Chen, R., Guo, C.-L., Zhou, J., 2013. Bioconversion characteristics of *Rhodopseudomonas palustris* CQK 01 entrapped in a photobioreactor for hydrogen production. Bioresour. Technol. 135, 331–338. https://doi.org/10.1016/j.biortech.2012.09.105.

Wang, Q., Shen, L., Zhao, Z., Yan, H., Xu, Q., Yin, C., Liu, X., Zhang, H., Liu, Y., 2018. Efficient culture of *Rhodopseudomonas palustris* using landfill leachate. J. Pure Appl. Microbiol. 12 https://doi.org/10.22207/JPAM.12.4.01.

Wang, R., Lin, C.-Y., Chen, S.-H., Lo, K.-J., Liu, C.-T., Chou, T.-H., Shih, Y., 2019a. Using high-throughput transcriptome sequencing to investigate the biotransformation mechanism of hexabromocyclododecane with *Rhodopseudomonas palustris* in water. Sci. Total Environ. 692, 249–258. https://doi.org/10.1016/j.scitotenv.2019.07.140.

Wang, Y., Tahir, N., Cao, W., Zhang, Q., Lee, D.-J., 2019b. Grid columnar flat panel photobioreactor with immobilized photosynthetic bacteria for continuous photofermentative hydrogen production. Bioresour. Technol. 291, 121806 https://doi.org/10.1016/j.biortech.2019.121806.

Wang, Z., Gao, D., Geng, H., Xing, C., 2021. Enhancing hydrogen production by photobiocatalysis through *Rhodopseudomonas palustris* coupled with conjugated polymers. J. Mater. Chem. A. https://doi.org/10.1039/D1TA01019K.

Wong, W.-T., Tseng, C.-H., Hsu, S.-H., Lur, H.-S., Mo, C.-W., Huang, C.-N., Hsu, S.-C., Lee, K.-T., Liu, C.-T., 2014. Promoting effects of a single *Rhodopseudomonas palustris* inoculant on plant growth by *Brassica rapa chinensis* under low fertilizer input. Microbes Environ. 29, 303–313. https://doi.org/10.1264/jsme2.me14056.

Wu, J., Wang, Y., Lin, X., 2013. Purple phototrophic bacterium enhances stevioside yield by *Stevia rebaudiana* Bertoni via foliar spray and rhizosphere irrigation. PLoS One 8, e67644.

Wu, P., Chen, Z., Zhang, Y., Wang, Y., Zhu, F., Cao, B., Wu, Y., Li, N., 2019. *Rhodopseudomonas palustris* wastewater treatment: Cyhalofop-butyl removal, biochemicals production and mathematical model establishment. Bioresour. Technol. 282, 390–397. https://doi.org/10.1016/j.biortech.2018.11.087.

Xiao, L., Zhao, Z., Ma, Z., Chen, J., Song, Z., 2020. Immobilization of *Rhodopseudomonas palustris* P1 on glass pumice to improve the removal of NH_4^+-N and NO_2^--N from aquaculture pond water. Biotechnol. Appl. Biochem. 67, 323–329. https://doi.org/10.1002/bab.1863.

Xing, D., Zuo, Y., Cheng, S., Regan, J.M., Logan, B.E., 2008. Electricity generation by *Rhodopseudomonas palustris* DX-1. Environ. Sci. Technol. 42, 4146–4151. https://doi.org/10.1021/es800312v.

Xu, W., Chai, C., Shao, L., Yao, J., Wang, Y., 2016. Metabolic engineering of *Rhodopseudomonas palustris* for squalene production. J. Ind. Microbiol. Biotechnol. 43, 719–725. https://doi.org/10.1007/s10295-016-1745-7.

Xu, J., Feng, Y., Wang, Y., Lin, X., 2018. Effect of rhizobacterium *Rhodopseudomonas palustris* inoculation on *Stevia rebaudiana* plant growth and soil microbial community. Pedosphere 28, 793–803. https://doi.org/10.1016/S1002-0160(18)60043-8.

Yang, C.F., Lee, C.M., 2011. Enhancement of photohydrogen production using *phbC* deficient mutant *Rhodopseudomonas palustris* strain M23. Bioresour. Technol. 102, 5418–5424. https://doi.org/10.1016/J.BIORTECH.2010.09.078.

Yin, L., Li, X., Liu, Y., Zhang, D., Zhang, S., Luo, X., 2012a. Biodegradation of cypermethrin by *Rhodopseudomonas palustris* GJ-22 isolated from activated sludge. Fresenius Environ. Bull. 21, 397–405.

Yin, Z.P., Shang, Z.W., Wei, C., Ren, J., Song, X.S., 2012b. Foliar sprays of photosynthetic bacteria improve the growth and anti-oxidative capability on Chinese dwarf cherry seedlings. J. Plant Nutr. 35, 840–853. https://doi.org/10.1080/01904167.2012.663439.

Zhai, Z., Du, J., Chen, L., Hamid, M.R., Du, X., Kong, X., Cheng, J., Tang, W., Zhang, D., Su, P., Liu, Y., 2019. A genetic tool for production of GFP-expressing *Rhodopseudomonas palustris* for visualization of bacterial colonization. AMB Express 9, 141. https://doi.org/10.1186/s13568-019-0866-6.

Zhang, J., Zhang, W.-X., Li, S.-Z., You, L., Zhang, C., Sun, C.-Z., Liu, X.-B., 2013. A two-step fermentation of distillers' grains using *Trichoderma viride* and *Rhodopseudomonas palustris* for fish feed. Bioprocess Biosyst. Eng. 36, 1435–1443. https://doi.org/10.1007/s00449-013-0887-5.

Zhang, S., Luo, X., Cheng, J., Peng, J., Zhang, D., Liu, Y., 2014. Genome sequence of pyrethroid-degrading bacterium *Rhodopseudomonas palustris* strain JSC-3b. Genome Announc. 2 https://doi.org/10.1128/genomeA.01228-13.

Zhang, D., Xiao, N., Mahbubani, K.T., del Rio-Chanona, E.A., Slater, N.K.H., Vassiliadis, V.S., 2015. Bioprocess modelling of biohydrogen production by *Rhodopseudomonas palustris*: Model development and effects of operating conditions on hydrogen yield and glycerol conversion efficiency. Chem. Eng. Sci. 130, 68–78. https://doi.org/10.1016/j.ces.2015.02.045.

Zhao, L., Zhao, C., Han, D., Yang, S., Chen, S., Yu, C.-P., 2011. Anaerobic utilization of phenanthrene by *Rhodopseudomonas palustris*. Biotechnol. Lett. 33, 2135. https://doi.org/10.1007/s10529-011-0681-x.

Zhao, C., Zhang, Y., Chan, Z., Chen, S., Yang, S., 2015. Insights into arsenic multi-operons expression and resistance mechanisms in *Rhodopseudomonas palustris* CGA009. Front. Microbiol. 6, 986. https://doi.org/10.3389/fmicb.2015.00986.

Zheng, Y., Harwood, C.S., 2019. Influence of energy and electron availability on *in vivo* methane and hydrogen production by a variant molybdenum nitrogenase. Appl. Environ. Microbiol. 85 https://doi.org/10.1128/AEM.02671-18 e02671–18.

Zuroff, T.R., Curtis, W.R., 2012. Developing symbiotic consortia for lignocellulosic biofuel production. Appl. Microbiol. Biotechnol. 93, 1423–1435. https://doi.org/10.1007/s00253-011-3762-9.