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MINI REVIEW

Prospective bioconversion of CO_2 and CO into fine chemicals via halophilic purple phototrophic bacteria

Samuel Stegman · Chrats Melkonian ·
Daniel Tamarit · Elisa Huang-Lin ·
Raquel Lebrero · Sara Cantera

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Abstract Microbial conversion of cheap and problematic carbon sources, like CO_2 and CO, into fine chemicals offers a promising green alternative to numerous traditionally fossil fuel-based industries such as steel, cement, and pharmaceuticals production. Purple phototrophic bacteria (PPB) are emerging as versatile key players in carbon–neutral systems due to their anoxygenic photosynthesis and diverse metabolic capabilities, enabling the transformation of carbon and nutrients into a wide range of valuable products. Traditionally positioned to treat organic carbon and produce medium-value products like bioplastics and biomass, PPB also exhibit autotrophic capabilities, enabling the valorization of waste gases, such as CO_2 and CO. A key strength of PPB is their metabolic and ecological diversity, including species inhabiting saline environments. Halophilic bacteria are known producers of valuable chemicals for pharmaceutical and medical applications, such as osmolytes (ectoine, hydroxyectoine), pigments, amino acids (proline) and natural coenzymes (ubiquinone), yet halophilic PPB remain underexplored in green upcycling processes. This study identified halophilic PPB capable of transforming waste gases into health and wellness products. Through a comprehensive literature review, we compiled a list of halophilic PPB and mined their genomes for genes linked to CO_2/CO utilization as carbon sources. Further genomic search revealed genes encoding enzymes for ectoine/hydroxyectoine, proline, ubiquinone, and carotenoids (lycopene, β-carotene, spirilloxanthin, and spheroidene). We identified 276 genomes of PPB with the genomic potential to valorise CO_2/CO into health-promoting ingredients, highlighting 22 species capable of producing three or more chemicals simultaneously. These findings highlight the untapped potential of halophilic PPB as bio-platforms for sustainable pharmaceutical production.

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S. Stegman (✉)
Australian Centre for Water and Environmental Biotechnology, The University of Queensland, Brisbane, QLD 4072, Australia
e-mail: samuel.stegman@uva.es

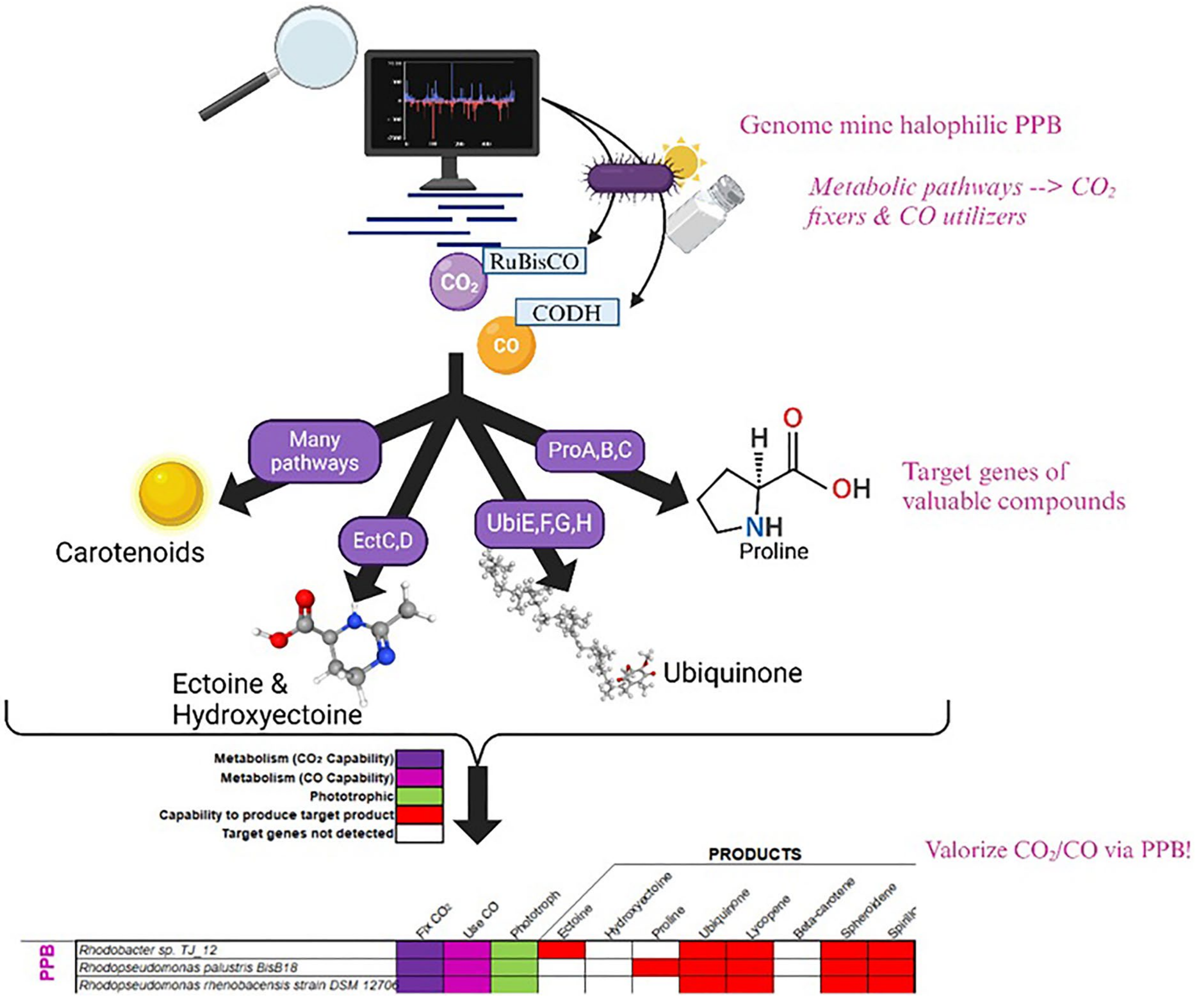
S. Stegman · E. Huang-Lin · R. Lebrero · S. Cantera (✉)
Institute of Sustainable Processes, University of Valladolid, Dr. Mergelina S/N., 47011 Valladolid, Spain
e-mail: sara.cantera@uva.es

S. Stegman · E. Huang-Lin · R. Lebrero · S. Cantera
Department of Chemical Engineering and Environmental Technology, University of Valladolid, Dr. Mergelina S/N., 47011 Valladolid, Spain

C. Melkonian · D. Tamarit
Theoretical Biology and Bioinformatics, Utrecht University, 3584CH Utrecht, The Netherlands

C. Melkonian
Bioinformatics Group, Wageningen University, Droevendaalsesteeg 1, 6708 PB Wageningen, The Netherlands

Graphical abstract



Keywords Carbon dioxide · Carbon monoxide · Halophiles · Health ingredients · Purple phototrophic bacteria

1 Introduction

The pharmaceutical industries generate more waste per unit product and byproduct than the oil refining, bulk, and fine chemical industries (Kar et al. 2022), while the iron and steel, and cement sectors generate significantly higher waste products such as CO_2 and CO than even the pharmaceutical industries, accounting for 7% and 5–8% of anthropogenic global CO_2, respectively (An et al. 2018; Kajaste and Hurme 2016; Nidheesh and Kumar 2019). These industries´ production output is set to rise over the next few years: the global pharmaceutical industry grows at 10% per annum (Gao et al. 2019; IQVIA (Statista), 2024;), while global cement, and steel production are set to increase by 50% and 30%, respectively, by 2050 (Monteiro et al. 2017; Yoro and Daramola 2020). As such, these industries face growing demands to minimize their environmental footprint and waste generation by adopting more sustainable practices. The pharmaceutical industry creates myriad, high market value products which can be used in diverse sectors such as cosmetics, medicines, traditional pharmaceuticals, and nutraceuticals. Although these products are industrially produced through unique pathways and technologies, they share some overarching similarities. The manufacturing of synthetic chemicals involves the use of costly and harmful aliphatic and aromatic compounds, includes a series of stepwise reactions to ensure their correct three-dimensional arrangement, and requires extensive purification steps that generate toxic waste and contribute to high greenhouse gas (GHG) emissions. Consequently, the production of synthetic chemicals fails to adhere to sustainability principles and is cost- and time-intensive. In response, the global market of green chemistry is increasing exponentially yearly and concerns about the effects and safety of synthetic substances for human consumption, along with green practices, drive demand for naturally sourced pharmaceutical and cosmetic ingredients (Mussagy et al. 2019; Ratti 2020). When considering industrial production of naturally sourced fine chemicals, some of them—such as lycopene or ubiquinone—rely on extraction from animal and plant tissues (Ciriminna et al. 2016). This approach involves ethical issues related to animal welfare, competition with the food market, and land scarcity due to large areas needed for crop cultivation (Li et al. 2020; Olufemi et al. 2009; Wu and Tsai 2013). Furthermore, the process waste generated requires treatment, which also results in high final costs (Vallecilla-Yepez and Ciftci 2018). In this context, microbial fermentation using specialized microorganisms emerges as a greener and potentially more commercially viable production process for these compounds (Alloun and Calvio 2024). It enables the sustainable production of high-purity, natural compounds without intensive consumption of natural resources (Li et al. 2020). This process is scalable, controllable, and can be sustained using widely available and cheap raw materials, ensuring consistent quality and yield (Ha et al. 2007; Hülsen et al. 2022; Wu and Tsai 2013). Microbial fermentation often uses mild operating conditions and simple reactors, compared to the more extreme operating conditions and multi-step process of chemical synthesis, to produce target compounds, and at times coproduce multiple compounds from the same carbon stock (Chen et al. 2024; Hara et al. 2014). In this regard, the capital and operating expenditure (CAPEX and OPEX), along with land requirement for this part of the process, could be reduced. It must be noted that downstream processes (e.g., product extraction, packaging and delivery) would still contribute to overall land area, production cost, and emissions. The economic feasibility of the process ultimately depends on the microbial production capacity and the market value of the product.

Microorganisms can generate numerous interesting health and wellness ingredients, including: carotenoids, such as beta-carotene, lycopene, spirilloxanthin, spheroidene; enzymes like ubiquinone (Coenzyme Q10); amino acids such as proline; and the compatible solutes ectoine and hydroxyectoine (Table 1). Table 1 lists bacteria which are currently employed in industry to produce specific valuable products and their role in nature and industrial uses.

Table 1 shows that some of these potentially valuable products, such as spheroidene and spirilloxanthin, still do not command an industry, much less one with microbial fermentation. This highlights a clear gap in the market, with Cahoon et al. (2012) showing that spirilloxanthin has higher antioxidant capacity than beta-carotene, and equals that of lycopene, which are both marketed as antioxidants. Nevertheless, the few current production processes for fine chemicals (via microbial fermentation) which do have an industry, rely on carbon sources such as glucose (or other sugars, yeasts, peptones). This dependency is costly, competes with the food market, and contributes to CO_2 emissions. Thus, to improve the competitiveness of industrial biotechnology in the health and wellness industries, it is essential to promote the development of novel circular economy systems. In this scenario, anaerobic biotechnology that harness green carbon and energy sources such as CO_2 and CO obtained from sectors such as cement and steel production, appear as an advantageous tool to promote valuable chemical production in a green way compared to synthetic processes. Furthermore, anaerobic processes can be more attractive than some aerobic processes, as they can treat compounds which are recalcitrant under aerobic conditions, and consume less energy (Shi et al. 2017; Xiao and Roberts 2010). Moreover, if these organisms grow under extremophilic conditions (e.g., high salinity), they would offer an extra advantage, requiring less freshwater and reducing the risk of contamination. Generally, saline wastewater has been observed to be inhibitory for conventional anaerobic treatment, however, anaerobic halophiles

Table 1 Bacteria currently used in industrial processes for the production of valuable compounds and their uses

Compound	Role in nature	Industrial Use	Market price* (USD kg^{-1})	Market size* (USD)	Current industrial production		References
					Bacteria	Carbon & Energy source	
ß-carotene	• Provitamin A (Vitamin A precursor)	• Food/feed industry: Additive, colorant. • Cosmetic industry: Skincare agent, creams, UV protection, anti-aging effects • Medical industry: Antioxidant, cardio-vascular, cataracts, anticancer • Health & nutraceuticals: Health benefits (e.g., prostate, mammary, & lung cancer, cardiovascular diseases)	400 – 2000	532M (CAGR^{+} of 6.7%)	Bacteria not used: *mostly fungi* & *microalgae*	Glucose (*fungi*) CO_2 + light (microalgae)	(Abu-Rezq et al., 2010; Grabowska et al., 2019; Viana et al., 2024)
Lycopene	• Photosynthesis • Photoprotection • Pigmentation		6000	145M (CAGR of 5.5%)	*Escherichia coli (E.coli)*	Glucose (and/or other sugars)	(Nandeshwar et al., 2024; Olempska-Beer, 2006; Sun et al., 2014; Vílchez et al., 2011)
Spheroidene			-	-	No industry yet	Organic acid, sugar + light	(Rodriguez-Concepcion et al., 2018)
Spirilloxanthin			-	-	No industry yet	Organic acids, sugars, alcohols, fatty acids + light	(Cahoon et al., 2012)
Ubiquinone	• Electron transport chain • Scavenges free oxygen radicals	• Health & nutraceuticals: Combat Parkinson's, Alzheimer's etc. • Cosmetic industry: Skincare	500-600	473.6M (CAGR of 4.8%)	*E. coli,* *S. cerevisiae*	Glucose (or other sugars)	(Allied Market Research, 2024; Capson-Tojo et al., 2020; He et al., 2021; Wu and Tsai, 2013)
Proline	• Osmo-protectant • Stabilise proteins & boost enzyme activity	• Food/feed industry: Additive, colourant. • Skincare agent	200-1000	330M (CAGR of 5.2%)	*C.glutamicum* *E. coli*	Glucose (at times with sucrose)	(Business Research Insights, 2024; Zhang et al., 2020)
Ectoine	• Osmo/thermo-protectant • Enzyme, DNA-protein nucleic acid stabilizer.	• Cosmetic industry: Skincare agent • Pharmaceutical industry: enhanced drug delivery	1000	10-20M (CAGR of 6.7%)	*H. elongata*	Glucose, sodium glutamate	(Kunte et al., 2014; Pérez et al., 2022;Verified Market Research, 2024)
Hydroxyectoine	• Stress protection (pH & oxidation)	• Skincare agent • Enhanced thermoplastic	>1000	-	No industry yet		(Pastor et al., 2010; Sauer and Galinski, 1998)

*Market data and price is for the current industry as some industries using bacteria do not currently exist or are dwarfed by those using microalgae. +Compound annual growth rates (CAGR) reported by market bodies

are well documented (Xiao and Roberts 2010). Photoautotrophic halophilic bacteria, in particular, hold promise due to their natural ability to synthesize pigments, osmolytes, and unique amino acids, thriving on CO_2 and inexpensive energy sources like CO and IR light. This approach reduces the carbon footprint and costs associated with traditional fermentation, promoting a greener, circular model for producing pharmaceuticals, medical products, and cosmetics.

2 Halophilic purple phototrophic bacteria as sustainable platforms to produce valuable products

Ecologically, halophilic microorganisms inhabit different ecosystems characterized by a salinity higher than seawater, i.e., 3.5% NaCl. They are physiologically diverse, appearing in a wide range of environments using different metabolisms; phototrophic, chemoorganotrophic and chemolithoautotrophic (Ventosa et al. 2011). Furthermore, they can be considered advantageous due to their low nutritional requirements, unlikely contamination under moderately aseptic conditions and genetic machinery. One of their mechanisms of halo-adaptation is based on the intracellular storage of unique biomolecules, extremolytes, which counteract the osmotic pressure of the external environment given by the high salinity (Bremer and Krämer 2019). Their useful properties have prompted extensive testing in recent years on human DNA, cells, and tissues, where they have demonstrated significant protective effects and potential medical and pharmaceutical applications. As a result, halophiles have gained recognition as valuable sources of bioactive compounds, specialized chemicals, and enzymes, positioning them as promising contributors to innovation in the health and wellness industries. Some of the most interesting extremolytes for the production of health and wellness chemicals with halophiles are ectoine, hydroxyectoine and proline, for which salinity is the main trigger for the expression of genes involved in their biosynthesis pathway (Argandoña et al. 2021). Halophiles in saline conditions are also shown to enhance their metabolite production as part of their broader stress response, regulated by environmental sensing pathways. Hence, high salinity may trigger carotenoid production in halophilic microorganisms as a protective mechanism against oxidative stress, UV and visible radiation, and osmotic pressure, while also stabilizing cell structures (de Lourdes Moreno et al. 2012). It is interesting to note, however, that the typical microbes used in industrial proline and carotenoid production are not halophilic. Replacing these microbes with halophilic bacteria could prove an efficient way to increase production capacity and reduce contamination, thereby improving chemical purity and lowering costs and resource consumption (Daoud and Ben Ali 2020). In this scenario, halophilic purple phototrophic bacteria (PPB) could be used to create a sustainable biorefinery using cheap carbon sources in the form of CO_2, and energy sources such as sunlight, H_2 or CO. PPB are a diverse group of anoxygenic phototrophs that harness solar light as an energy source (Hülsen et al. 2014). PPB's demonstrated benefits confirm their distinctive potential as promising candidates for cell platforms. These advantages include their widespread presence across varied and, at times, extreme ecosystems, ranging from soil, freshwater, wastewaters, and saline and marine environments, which facilitate synthetization of a diverse array of bioproducts, holding significant market potential across various industries (Capson-Tojo et al. 2020). This versatility is enhanced by their taxonomic diversity, as PPB encompass a polyphyletic set of microorganisms—at around 50 known genera of anoxygenic PPB and 75 known PPB genera in total—belonging to multiple lineages within the phylum Proteobacteria (Madigan and Jung 2009). Their unique light absorption characteristics, specifically in the near-infrared spectrum (>805 and >1000 nm) through bacteriochlorophylls (BChls) and in the visible range (400–600 nm) via a varied array of carotenoids, negates competition with other phototrophs, reduces costs (Seto et al. 2020), and can have a 1:1 substrate-to-biomass conversion (Alloul et al. 2019). Their anoxygenic metabolism negates the need of aeration which could reduce the OPEX (Capson-Tojo et al. 2021).

Within their spectrum of metabolic pathways, several PPBs can grow purely autotrophically, using CO_2 as the carbon source in the presence of infrared light. Moreover, some PPBs have demonstrated the ability to oxidize inorganic compounds like CO or H_2, with and without light. For instance, studies have reported the capability of *Rubrivivax gelatinosus* CBS, a purple non-sulfur bacterium, of using CO as the only carbon source under anaerobic light conditions. Moreover, in the absence of light, it exhibits the ability to utilize CO as both the carbon and energy source (Wawrousek et al. 2014). Similarly, Dhakal and Acharya (2021) reported *Rhodospirillum rubrum* to have the inherent ability to fix syngas via CO and H_2 oxidization and CO_2 fixation.

Moreover, PPB are becoming important in bioprospecting. PPB such as *Rhodobacter capsulatus* and *Rhodospeudomonas palustris* are well studied and recognised as important microbial mediators due to their production of PHAs, high-protein biomass, and carotenoids on a wide range of organic and inorganic carbon substrates (Capson-Tojo et al. 2020), and they have also been suggested for saline and hypersaline wastewater bioremediation due to their salt-tolerance (Grattieri et al. 2019; Labarile et al. 2021). Furthermore, it is important to note, the valuable osmolyte, ectoine, was first discovered in the PPB *Ectothiorhodospira* (Galinski et al. 1985). However, it has not yet been produced continuously, at scale, with PPB; this represents a missed opportunity. All these characteristics make PPB exceptional microbes for valorizing industrial gases into highly valuable chemicals for the pharmaceutical, medical and cosmetic industries.

3 Potential halophilic purple phototrophic bacteria able to produce carotenoids, osmolytes, amino acids and co-enzymes from green carbon and energy sources

Although several PPB can grow autotrophically, some utilize CO, and various strains are halophilic, the potential of harnessing halophilic PPB to produce valuable chemicals from CO_2 and CO under high-salinity conditions remains largely unexplored. A literature review of primarily PPB uncovered ~ 100 potentially halophilic species. Supplementary materials shows the recorded phenotypes, environment and optimal growth conditions and growth modes. The genomes of such PPB were gathered from public databases (Bacterial and Viral Bioinformatics Resource Center (BV-BRC; https://www.bv-brc.org/) and the National Center for Biotechnology Information (NCBI, https://www.ncbi.nlm.nih.gov/)) and then expanded to 2661 genomes targeting 94 genera. Genome retrieval and bioinformatics analysis used a specifically updated methodology from Hrovat et al., (2024) and Melkonian et al., (2019) for this study (see supplementary materials and the GitHub repository). The list of bacteria (phototrophs and non-phototrophs, PPB and non-PPB) was expanded based on their evolutionary roots and phylogenetic relations with the PPB gathered from literature with the end goal of capturing any PPB missed by the original literature review. After quality control filtering, duplicate removal, and manual curation, 1348 genomes remained (see supplementary materials). In total, 1086 genomes were classified as halophilic/halotolerant. We predicted gene/protein sequences with the gene prediction algorithm Prodigal (PROkaryotic DYnamic programming Gene-finding ALgorithm) (Hyatt et al. 2010). We performed functional annotation with eggnog (Cantalapiedra et al. 2021) with the following modifications to the default parameters. First pass genome mining was conducted to assess which of those microorganisms were autotrophs, carboxydotrophs or carboxydovores. For CO_2 fixation, the pathways (and target genes and orthologs within the pathway) considered were the reductive pentose phosphate (Calvin) cycle, reverse tricarboxylic acid (rTCA) cycle, and the Wood-Ljungdahl pathway. For CO utilization, we targeted the KO orthologs of the CO dehydrogenase. The identified genomes that were reported to have the genetic potential to use CO_2 and CO are summarized in supplementary materials (Table S1). The resulting genomes were mined for the presence of certain gene clusters and orthologs within predefined metabolic pathways (see Fig. 1, Table S2, and Fig. S3), such as: the amino acid proline; pigments/carotenoids such as lycopene, beta-carotene, spirilloxanthin, spheroidene; the osmolytes ectoine and hydroxyectoine; and the co-enzyme ubiquinone. We found a total of 300 genomes encoding genes for CO_2 fixation with at least one of these pathways, and 132 genomes that had the genes that codify for CO dehydrogenases. Of these genomes, 13 encode genes for the use of both compounds as carbon and energy source. PPB genomes accounted for > 90% of the 300 CO_2-fixing bacteria identified. On the other hand, they represented only 18% of the 132 CO-utilizing bacteria. Importantly, all 13 genomes which overlapped CO_2 fixation and CO utilization belonged to PPB.

Genome mining resulted in 276 genomes of PPB and 69 genomes of non-PPB which potentially have the ability to fix CO_2 and/or utilize CO while producing at least one product. 264 PPB and 4 non-PPB genomes potentially have the ability to fix CO_2 and produce one or more products, and 20 PPB and 65 non-PPB genomes have the genomic potential to utilize CO and produce one or more products. The PPB and non-PPB genomes which have the genetic potential to fix CO_2 and produce at least one desired compound, and utilize CO and produce at least one desired compound, are listed in supplementary materials.

We collated and grouped the genomes based on their abilities to produce the different desired, valuable compounds. To be shortlisted as potentially industrially relevant strains (Fig. 2), the organisms needed to satisfy selection criteria, meeting at least 4 conditions (capability for C_1 metabolism and synthesis of 3 products), with joint CO_2 and CO utilization being prized. The analysis uncovered a total of 22 PPBs and 5 non-PPB strains which could potentially utilize CO_2 and/or CO and produce several valuable products (see Fig. 2; see supplementary materials for all genomes which did not meet selection criteria). Of the 13 strains which could utilize both CO_2 and CO as

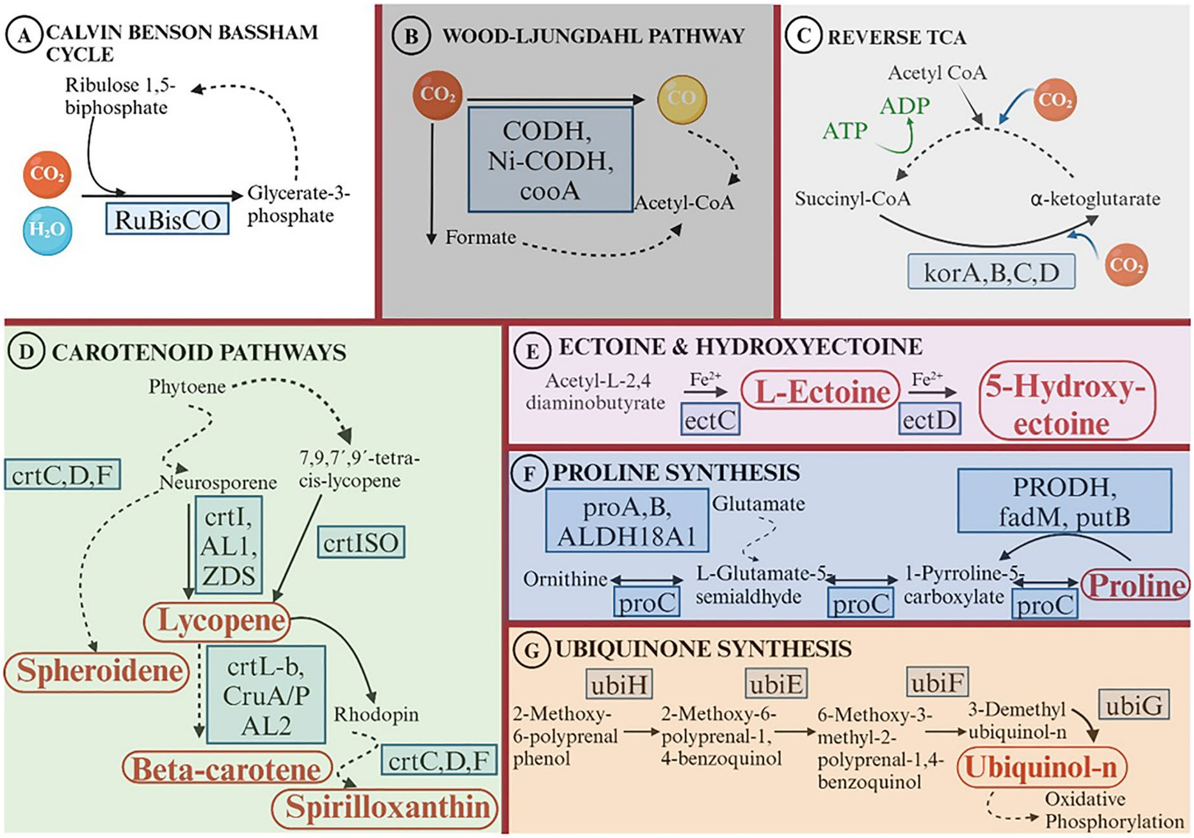
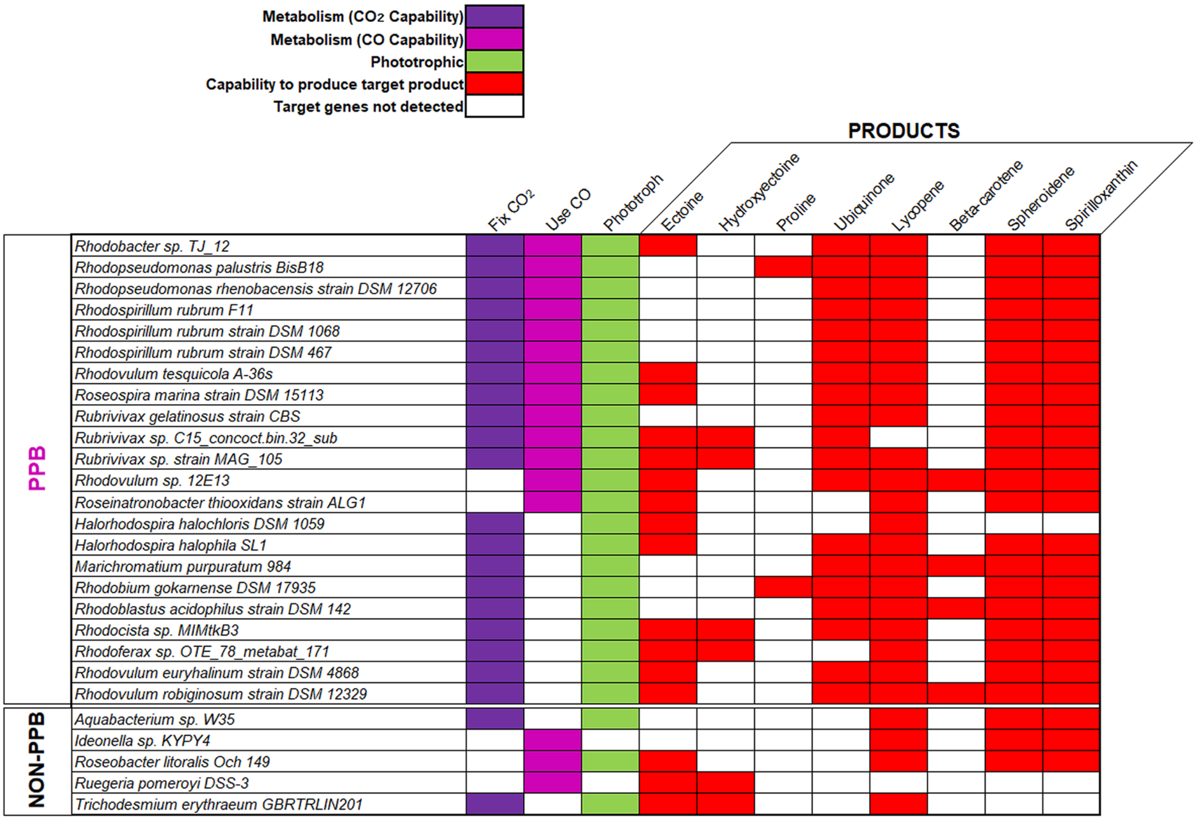


Fig. 1 Metabolic and biosynthesis pathways for PPB. The three metabolic pathways considered are (**A**) the Calvin Benson-Bassham cycle, (**B**) the Wood-Ljungdahl pathway, and (**C**) the reverse TCA cycle. Note, the relevant gene expressions are within blue boxes, solid arrows represent a direct pathway, and dotted arrows represent a longer pathway which may contain intermediates not depicted. The products (bold, red text, with red border) are shown in (**D**) carotenoid pathways, (**E**) ectoine and hydroxyectoine biosynthesis, (**F**) proline, and (**G**) ubiquinone

carbon and energy sources (all PPB), 11 strains met the selection criteria and have the genes capable of producing multiple high-value compounds. Analysing the shortlist in Fig. 2, the 22 PPB strains (which can utilise CO_2 or CO and produce valuable products) include 12 halotolerant (belonging to the genera *Rhodobacter, Rhodoferax, Rhodopseudomonas, Rhodospirillum,* and *Rubrivivax*), 8 halophilic (e.g., *Halorhodospira, Rhodobium, Rhodovulum, Roseinatronobacter, Roseospira*, *Marichromatium*), and 2 salt-tolerating, though mainly freshwater (genera *Rhodoblastus* and *Rhodocista*) bacteria. Of the 5 non-PPB strains which could utilize CO_2 or CO, *Aquabacterium* sp. W35 and *Trichodesmium erythraeum* GBRTRLIN201 are halophiles, *Roseobacter litoralis* Och 149 and *Ruegeria pomeroyi* DSS-3 are halotolerant, and *Ideonella* sp. KYPY4 is a predominately freshwater bacterium. One limitation to the method which must be addressed is the presence of incomplete strains and bins (e.g., *Rubrivivax* sp. C15_concoct.bin.32_sub), within the databases, which, while they are reported to have potential functionality, are not able to be used immediately.

When considering just strains with the ability to fix CO_2 (Fig. S4), the bioinformatics analysis detected: 57 strains with the potential to produce ectoine (e.g., *Halorhodospira halochloris* and *Rhodovibrio salinarum*); 11 hydroxyectoine-producing microorganisms (10 PPBs including species from the genera *Rubrivivax*, *Rhodocista,* and *Rhodoferax*); 4 proline-producing microorganisms (3 PPB: *Rhodobium* spp. and *Rhodopseudomonas palustris*); 240 ubiquinone-producing bacteria, including *Halorhodospira* spp., *Marichromatium* spp., and *Rhodobacter* spp.; 222



Metabolism (CO_2 Capability)	🟪
Metabolism (CO Capability)	🟣
Phototrophic	🟩
Capability to produce target product	🟥
Target genes not detected	⬜

		Fix CO_2	Use CO	Phototroph	Ectoine	Hydroxyectoine	Proline	Ubiquinone	Lycopene	Beta-carotene	Spheroidene	Spirilloxanthin
					PRODUCTS							
PPB	*Rhodobacter sp. TJ_12*	🟪	🟣	🟩	🟥	⬜	⬜	🟥	🟥	⬜	🟥	🟥
	Rhodopseudomonas palustris BisB18	🟪	🟣	🟩	⬜	⬜	🟥	🟥	🟥	⬜	🟥	🟥
	Rhodopseudomonas rhenobacensis strain DSM 12706	🟪	🟣	🟩	⬜	⬜	⬜	🟥	🟥	⬜	🟥	🟥
	Rhodospirillum rubrum F11	🟪	🟣	🟩	⬜	⬜	⬜	🟥	🟥	⬜	🟥	🟥
	Rhodospirillum rubrum strain DSM 1068	🟪	🟣	🟩	⬜	⬜	⬜	🟥	🟥	⬜	🟥	🟥
	Rhodospirillum rubrum strain DSM 467	🟪	🟣	🟩	⬜	⬜	⬜	🟥	🟥	⬜	🟥	🟥
	Rhodovulum tesquicola A-36s	🟪	🟣	🟩	🟥	⬜	⬜	🟥	🟥	⬜	🟥	🟥
	Roseospira marina strain DSM 15113	🟪	🟣	🟩	🟥	⬜	⬜	🟥	🟥	⬜	🟥	🟥
	Rubrivivax gelatinosus strain CBS	🟪	🟣	🟩	⬜	⬜	⬜	🟥	🟥	⬜	🟥	🟥
	Rubrivivax sp. C15_concoct.bin.32_sub	🟪	🟣	🟩	🟥	🟥	⬜	🟥	⬜	⬜	🟥	🟥
	Rubrivivax sp. strain MAG_105	🟪	🟣	🟩	🟥	🟥	⬜	🟥	🟥	⬜	🟥	🟥
	Rhodovulum sp. 12E13	⬜	🟣	🟩	🟥	⬜	⬜	🟥	🟥	🟥	🟥	🟥
	Roseinatronobacter thiooxidans strain ALG1	⬜	🟣	🟩	🟥	⬜	⬜	⬜	🟥	⬜	🟥	🟥
	Halorhodospira halochloris DSM 1059	🟪	⬜	🟩	🟥	⬜	⬜	⬜	🟥	⬜	⬜	⬜
	Halorhodospira halophila SL1	🟪	⬜	🟩	🟥	⬜	⬜	🟥	🟥	⬜	🟥	🟥
	Marichromatium purpuratum 984	🟪	⬜	🟩	⬜	⬜	⬜	🟥	🟥	🟥	🟥	🟥
	Rhodobium gokarnense DSM 17935	🟪	⬜	🟩	⬜	⬜	🟥	🟥	🟥	⬜	🟥	🟥
	Rhodoblastus acidophilus strain DSM 142	🟪	⬜	🟩	⬜	⬜	⬜	🟥	🟥	🟥	🟥	🟥
	Rhodocista sp. MIMtkB3	🟪	⬜	🟩	🟥	🟥	⬜	🟥	🟥	⬜	🟥	🟥
	Rhodoferax sp. OTE_78_metabat_171	🟪	⬜	🟩	🟥	🟥	⬜	⬜	🟥	⬜	🟥	🟥
	Rhodovulum euryhalinum strain DSM 4868	🟪	⬜	🟩	🟥	⬜	⬜	🟥	🟥	⬜	🟥	🟥
	Rhodovulum robiginosum strain DSM 12329	🟪	⬜	🟩	🟥	⬜	⬜	🟥	🟥	🟥	🟥	🟥
NON-PPB	*Aquabacterium sp. W35*	🟪	⬜	🟩	⬜	⬜	⬜	⬜	🟥	⬜	🟥	🟥
	Ideonella sp. KYPY4	⬜	🟣	⬜	⬜	⬜	⬜	⬜	🟥	⬜	🟥	🟥
	Roseobacter litoralis Och 149	⬜	🟣	🟩	🟥	⬜	⬜	⬜	🟥	⬜	🟥	🟥
	Ruegeria pomeroyi DSS-3	⬜	🟣	⬜	🟥	🟥	⬜	⬜	⬜	⬜	⬜	⬜
	Trichodesmium erythraeum GBRTRLIN201	🟪	⬜	🟩	🟥	🟥	⬜	⬜	🟥	⬜	⬜	⬜

Fig. 2 Shortlist of halotolerant and halophilic PPB and non-PPB which are able to use CO_2 and/or CO to produce an array of valuable products

spirilloxanthin/spheroidene producing PPB (out of 223 microorganisms); 3 beta-carotene-producing species (*Marichromatium purpuratum*, *Rhodoblastus acidophilus*, and *Rhodovulum robiginosum*); and 244 lycopene-producing microorganisms.

With regard to CO-utilizers (Fig. S5), the list is more succinct. Only *Rhodovulum* sp. could produce beta-carotene; *Rhodopseudomonas palustris* BisB18 was the only proline producer; 54 bacteria could produce ectoine (predominately aerobic bacteria such as *Ruegeria* and *Roseobacter* alongside 6 PPBs including *Rhodobacter* sp., *Roseospira marina*, and *Rhodovulum* spp.); *Rubirvivax* sp. and *Ruegeria pomeroyi* were the species which could produce hydroxyectoine; 18 organisms (all PPB, including species from *Rhodospirillum*, *Rhodovulum*, and *Rubrivivax*) could produce ubiquinone; and 38 microorganisms (16 PPBs including species from the genera *Rhodobacter*, *Rhodospirillum*, and *Rubrivivax*) could produce spheroidene and spirilloxanthin.

When considering the non-PPB strains which could be utilized to produce high value products via CO_2 and CO, there are no strains with the ability to fix CO_2, utilize CO, and produce any value-added product in our collection (Fig. S6). Analyzing the strains which have the capacity for CO_2 fixation: *Trichodesmium erythraeum* GBRTRLIN201 has the ability to produce ectoine and hydroxyectoine; *Trichodesmium erythraeum* GBRTRLIN201, *Desulfofustis* sp. PB-SRB1, and *Aquabacterium* sp. W35 have the ability to produce lycopene; *Fermentimonas caenicola* strain MAG2 is the only proline producer; *Aquabacterium* sp. W35 is the only spheroidene and spirilloxanthin producer; and no strains produce ubiquinone or beta-carotene. When considering the strains which have the ability to utilize CO, the list of products becomes more extensive. 48 strains (predominately belonging to the genera *Ruegeria, Roseobacter*, and *Leisingera*) have the ability to also produce ectoine. Only *Ruegeria pomeroyi* DSS-3 can also produce hydroxyectoine. The lycopene (17 strains) and spirilloxanthin/spheroidene (14 strains) producers consisted mainly of *Ideonella* sp., *Roseinatronobacter thiooxidans*, *Roseobacter* sp., and *Thalassobacter* sp. No non-PPB strains recorded the ability to utilize CO and produce proline, ubiquinone, or beta-carotene.

While this study focussed primarily on PPB, non-PPB genomes (evolutionarily related to PPB) were also shown. However, this list did not incorporate all photosynthetic organisms and it is recognised that other non-PPB phototrophs (e.g., algae) and aerobic bacteria (e.g., cyanobacteria) also produce various compounds. Regarding ectoine and hydroxyectoine, algae do not have the genomic potential required to produce it, as the genes are found almost exclusively in *Bacteria* (Widderich et al. 2014). Some cyanobacteria do have the ability to produce it (Dong et al. 2023). Regarding ubiquinone, algae, such as *Porphyridium purpureum*, and cyanobacteria can produce it (Degli Esposti 2017; Klein et al. 2012). Both algae and cyanobacteria, for example *Chlamydomonas reinhardtii, Chlorella* sp.*, Nostoc muscorum*, are capable proline producers (Barera and Forlani 2023; Chua et al. 2020). With regards to carotenoids, algae and cyanobacteria are famed for production of pigments, possessing the genomic potential to produce diverse carotenoids—with 200 carotenoids found in algae—including beta carotene and lycopene (Egeland 2016). Although to our knowledge, algae and cyanobacteria do not produce the carotenoids spheroidene and spirilloxanthin.

4 Perspectives

Genome mining of previously unconsidered microorganisms, such as halophilic PPB, which convert CO_2 and CO gases into valuable natural chemicals, can be of great interest for society, the health and wellness industries, and the economy. However, both the development of new industries, and the initial phase of genome mining face significant challenges which must be addressed.

4.1 Perspectives on new industries

Reimagining these waste gases – CO_2/CO sourced from previously unconsidered emitters, *e.g.,* steel and coke mills, cement production, biogas and biomass gasification, and crude oil refineries – as viable carbon sources for bioconversion processes, the health and wellness industries could become new carbon scrubbing stations and adhere to emissions targets as outlined in Europe's *Green Deal* and *The Paris Agreement*. Various industries could sell their carbon byproducts (e.g., CO_2) to nearby biorefineries producing the fine chemicals, or incorporate the PPB treatment technology into their own business model, valorizing the waste gases into valuable chemicals of industrial importance as an additional profit stream. However, these aforementioned industries produce waste gases of varying chemical compositions: the CO_2 concentration in steel and cement gas (20–30% (v/v)) differs from that in power plant emissions (12–15% (v/v)) (Baker et al. 2018). Additionally, gases like O_2, CH_4, NO_x, and SO_x can also be present at varying levels. This variability could determine which specific PPB species or consortia are best suited, and may require upfront treatment such as gas separation membranes, scrubbing or O_2 purging. Acknowledging this, PPB are extremely robust, perform denitrification, utilize sulfides, sulfates, and reduced sulfur compounds (Madigan and Jung 2009). This suggests that these trace pollutants may not affect PPB´s growth kinetics. Gabrielli et al. (2020) compared traditional chemical industries against those utilizing direct air captured carbon sources (such as CO_2 to produce MeOH) in a CCU design and highlighted a major drawback if the system is to be run at net-zero carbon: the need for sustainable H_2, which typically has a significantly larger land footprint—requiring 20 times more space than some renewable systems for direct air capture. However, if H_2 does not need to be produced separately and is already present in the waste gas (e.g., syngas) at a point source, this could save on land, energy and reagents. Regarding how these systems could look, in terms of land footprint and CAPEX, it must be stated that there is a lack of a) data on large-scale, industrial PPB processes, and b) consensus on ideal photobioreactor (PBR) design or economics (Hülsen et al. 2022). This means economic analyses must be treated with caution, with significant work still needed to determine its economic feasibility. While not directly translatable technologies, algae are the most relevant, comparable microorganisms and we can use this as a starting point for comparison. Algae do have some industries producing valuable compounds: depending on the desired product, large open ponds or compact PBRs are used. Alloul et al. (2021) showed that the CAPEX of closed tubular PBRs was 80–90 times higher than open raceways. Nevertheless, closed sterilized systems must be used for pharmaceutical products, especially given PPB's anaerobic requirement. It has been postulated that PPB´s CAPEX could theoretically be 3–10 times smaller than that of algae due to factors such as faster PPB growth rates and higher biomass concentrations (Hülsen et al. 2022), however this compares heterotrophs against autotrophic algae. Under autotrophic metabolism, PPB´s growth rate is slower, comparable to that of algae (Lee et al. 2022; Singh and Singh 2015). The harvesting cost of microalgae (30% of the total process) (Alabi et al. 2009) would likely be similar for PPB, unless a biofilm growth method is employed which can concentrate the biomass 100 fold, thereby negating some dewatering cost (Hülsen et al. 2020). If we consider PPB´s compact bioreactor design (vertical integration) and a point-source CO_2/H_2 gas supply, the land footprint could become more comparable to current pharmaceutical plants, especially if redundant traditional units (e.g., high-temperature, pressurized reactors, multi-step reaction processes) are eliminated. On a broader note for industry, the high salinities enable the use of seawater, negating sterilization processes, conserving freshwater stocks, repurposing arid land, and offering countries which have reliable seawater access, but limited freshwater supplies a chance to develop new industries.

4.2 Perspectives on the tool of genome mining

Before such industries can be created, significant work is still required. Firstly, not all bacteria are available as complete, isolated strains, and the cultivation of these strains could be a bottleneck. Secondly, experimentally verifying the link between genotype and phenotype and then translating the discovery to new biotechnological applications entails numerous developmental and regulatory hurdles, which must not be understated. The presence of a specific gene does not guarantee the production of a target compound, as it may not be functional, or actively expressed, and as such, wet-lab validation is essential to confirm that the organism can utilize the gene. To conclude, while considerable work remains, this research potentially provides a new avenue to develop circular, green industries using natural, halophilic, microbial processes which eliminate waste gases like CO_2 and CO.

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Author contributions S.S conducted the initial literature review, wrote the main manuscript and supplementary materials text, prepared the figures and table, and conducted data analysis and interpretation. C.M performed the major bioinformatics analysis/genome mining , code generation, and figure generation present in the GitHub depository. E.H assisted with the initial literature review. D.T contributed to bioinformatics analysis and reviewed the manuscript. R.L provided extensive feedback on editing and refining the manuscript. S.C. participated in the conceptualization, writing and validation and funding acquisition.

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Data and code availability Supporting material can be found in the Supplementary Materials. The code, source data, and processed tables necessary to reproduce the results are available at: https://github.com/Chrats-Melkonian/Genome_mining_PPB_Halo.git.

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article. Views and opinions expressed are those of the authors only and do not necessarily reflect those of the European Union. Neither the European Union nor the granting authority can be held responsible for them. The authors have no relevant financial or non-financial interests to disclose.

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