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Harnessing cyanobacteria for a greener tomorrow: CO_2 mitigation and bioconversion to sustainable chemicals and fuels

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ABSTRACT

The depletion of fossil fuels and the escalating impact of climate change have driven the search for sustainable energy alternatives. Bioenergy has emerged as a promising substitute; however, first- and second-generation biofuels pose concerns regarding food security and water scarcity. In contrast, third-generation biofuels derived from cyanobacteria and microalgae offer viable solutions due to their ability to fix carbon dioxide (CO_2), thrive in non-arable lands, exhibit rapid growth, and produce high lipid yields for biofuel extraction. This review explores the production of biodiesel, biomethane, biohydrogen, and bioethanol from these microorganisms. Furthermore, it discusses advancements in biotechnology that enhance biofuel yield, evaluates the challenges and possibilities associated with these methods, and highlights the role of cyanobacteria and microalgae in eco-friendly biomass production and CO_2 sequestration. By integrating sustainable biotechnology, these microorganisms contribute to the development of renewable energy while mitigating environmental concerns, paving the way for a greener and more sustainable future.

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Introduction

The energy crisis has threatened the world due to the depletion of natural resources, such as fossil fuels. On the other hand, the combustion of fossil fuels releases a substantial amount of carbon dioxide into the atmosphere, contributing to global warming and various environmental issues. Hence, there is a need for an alternative renewable resource that meets the world's energy demand (Gouveia & Oliveira, 2009, Moharam et al. 2023, Subramanian & Suresh 2025).. High energy demands have been increasing due to climate change, fossil fuel scarcity, and global warming, among other factors. Lately, researchers have focused on the biological conversion of CO_2 into value-added chemicals and fuels (Jena et al., 2012). Since fossil fuels are depleting day by day, when they are combusted, a large amount of 73% of CO_2 is released into the atmosphere. In the 20th century Earth's average temperature increased up to 0.6°C as revealed by the Intergovernmental Panel on Climate Change (IPCC) this is caused by the emission of carbon dioxide into the atmosphere led Earth's temperature increase from 1.5 °C to 4.5°C in the year 2100 which led to hurricane and flooding are the most common occurrence (M. R. Ananadhi Padmanabhan, 2012). There is a need to reduce the emission of CO_2 into the atmosphere, and

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the dwindling reserves of crude oil, chemicals, and biofuels are an attractive energy source for fuel production. The emission of greenhouse gases and the substitution of fossil fuels are the most essential components of bioenergy (Kulkarni & Dalai, 2006). Cyanobacteria provide an effective platform that utilises most of the renewable energy in the form of CO_2, converting it into value-added products, and uses sunlight as the primary energy source.

Utilisation and resulting carbon-capturing technologies play a significant role in mitigating the hazardous effects of elevated CO_2 levels, and this technology is an advanced technique for industrial-scale applications. To overcome these technological problems, cyanobacterial-based products are most commonly used. Cyanobacteria are historical photosynthetic prokaryotes that might be the progenitors of the plant chloroplast. Cyanobacteria can grow in various conditions, including water, and under diverse conditions (Brian ALAN Whitton, 2002). Primarily, cyanobacteria are responsible for photosynthesis, generating oxygen (Hamilton et al., 2016). Currently, 25% of the planet's primary productivity is attributed to cyanobacteria, with approximately two-thirds of this productivity occurring in the ocean (Brian ALAN Whitton, 2002; Hamilton et al., 2016). The main merit of photosynthetic prokaryotic cyanobacteria is that they utilise carbon dioxide and convert it into value-added chemicals and fuels. Photosynthesis, utilised by cyanobacteria, involves the reductive pentose phosphate pathway, which produces biomass by using CO_2 and sunlight as carbon and energy sources (Figure 1).

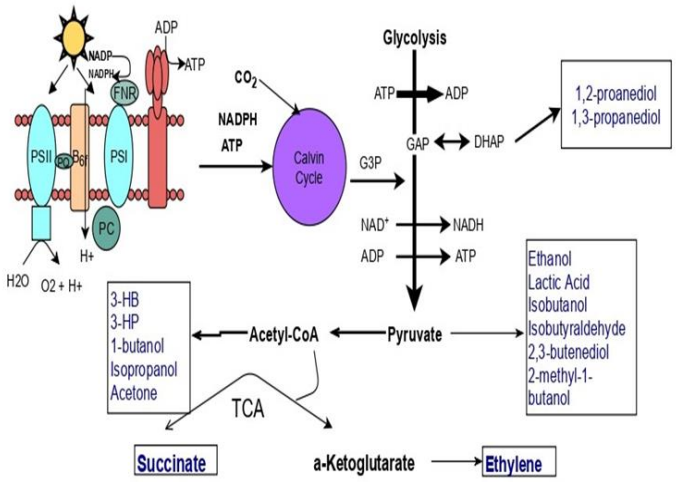

Fig 1. Overview of Cyanobacterial chemical production using photosynthetic metabolism

Various types of biofuels can be produced from blue-green algae (Bullerjahn & Post, 2014; Flombaum et al., 2013). Cyanobacteria have a greater ability to capture solar energy compared to plants, which convert only 9% of the solar energy into biomass (Hankamer et al., 2007; Hu et al., 2008). Likewise, cyanobacteria protect their carbon through a bicarbonate intermediate, which is utilized for carbon development by the expansion of bicarbonate derived from atmospheric CO_2 (or) emitted CO_2 from industrial sources (Chi et al., 2011). Cyanobacteria will grow faster than other higher plants. Most cyanobacteria consume a higher amount of CO_2, resulting in the production of useful products. Similarly, it isn't easy to modify the genetic characteristics of most prokaryotes, but in cyanobacteria, it is relatively easy to alter the metabolic pathway. In eukaryotic algae, the genetic complexity in the metabolic pathway is more challenging (Gimpel et al., 2015). The cultivation of cyanobacteria is primarily conducted in bioreactors on land that is not suitable for farming, which helps control competition with other food crops (Chi et al., 2011; Gimpel et al., 2015; Pate et al., 2011). The present review paper describes the production of biofuels and other value-added products using various cyanobacterial species. It mainly focuses on (i) dihydroxyacetone phosphate and pyruvate-derived products, (ii) malonyl-CoA-derived products, (iii) high-value-added natural products, and (iv) fuel-like isoprenoid and bisabolene products.

Biochemical and Biofuel Production using CO_2-Tolerant Cyanobacterial Species

Dihydroxyacetone Phosphate and Pyruvate Derived Products

Dihydroxyacetone phosphate (DHAP) and pyruvate are placed near the area of the basic carbon-fixation responses and are produced from glyceraldehyde-3-phosphate (GAP) (Fig. 2) through one or five chemical steps, respectively. High levels of chemicals are made from DHAP and pyruvate, out of which high levels of alcohol are produced by cyanobacteria (Atsumi et al., 2009; Deng & Coleman, 1999; Hirokawa et al., 2017; Oliver et al., 2013; Shen & Liao, 2012). During active photosynthesis, a high concentration of pyruvate is formed; however, in some pathways, early irreversible decarboxylation is present. In such cases, NADPH is primarily utilized as a redox cofactor, and it is abundantly available during the photoautotrophic growth of plants. Biosynthetic pathways of *S. elongatus* 7942 results in the production of 1,3-propanediol(Hirokawa et al., 2016). Generally, in the cyanobacteria cycle, DHAP is converted into glyceraldehyde-3-phosphate by the enzyme GAP

dehydrogenase. Accordingly, GAP dehydrogenase is formed from glycerol by the enzyme phosphatase, which converts glycerol into 3-hydroxypropionaldehyde via the coenzyme B12-dependent glycerol dehydratase. Using a cyanobacterial strain, 288 mg/L of 1,3-propanediol was obtained after 14 days, with an average productivity of 0.9 mg/L/h under continuous light conditions (Deng & Coleman, 1999).

Fig 2. Metabolic pathway of Dihydroxyacetone Phosphate into Glyceraldehyde 3-phosphate (GAP)

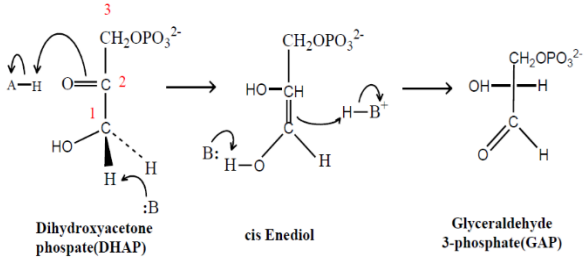

Table 1. Biofuels produced by Cyanobacteria

Chemical	Titer value	References
C_2H_5OH	54 nmol L/d	Deng and Coleman 1999
$C_4H_{10}O$	450 mg/L	Atsumi et al., 2009, Li et al., 2014
C_3H_8O	288 mg/L	Hirokawa et al., 2016 Kusakabe et al., 2013
$C_3H_8O_2$	1.22 g/L	Hirokawa et al., 2016 Hirokawa et al., 2017
$C_3H_6O_3$	837.18 mg/L	Wang et al., 2013 Lan et al., 2015

Bioethanol is produced using the decarboxylation of pyruvate to acetaldehyde and the reduction of acetaldehyde into bioethanol. An 83% increase in bioethanol production rate was achieved using the *Synechocystis species* (Fig.3). Generally, two molecules of acetyl-CoA are reduced to form acetoacetyl-CoA, which is then transesterified with acetic acid to yield acetoacetate. Acetyl-CoA subsequently leads to the production of value-added chemicals and fuels. Cyanobacteria require dark and anaerobic conditions for the activation of glycolytic pathways (Hirokawa et al., 2015; Kusakabe et al., 2013). For the conversion of acetate and acetyl-CoA, a dark phase of five days is required to produce isopropanol, and ten light phases are needed, which serve as the precursor for isopropanol production. In the *S. elongatus* 7942 biosynthetic pathway, 146 mg/L of isopropanol was produced, with an average production rate of 0.6 mg/L/h (Atsumi et al., 2009). Isobutanol-derived esters are primarily used as plasticisers for polymers (Carroll et al., 2016; Rodriguez et al., 2014). 2-Ketoisovalerate (KIV) is an intermediate in native L-valine biosynthesis. Isobutyraldehyde is formed by the decarboxylation of 2-ketoisovalerate (KIV) and then reduced to isobutanol (Atsumi et al., 2009). The mutant of glycogen synthase (DglgC) of 7942 enhances the production quantity of isobutanol by up to 52%, and growth is inhibited due to the deletion of glgC under high light conditions without this pathway (Li et al., 2014). CO_2-engineered microorganisms of *Synechococcus elongatus* PCC7942 species were used for the production of 2,3-Butanediol (2,3-BD) (Oliver et al., 2014). Similarly, dehydration of 2,3-butanediol (2,3-BD) forms the precursor of polymers such as 1,3-butadiene, the drop-in fuel additive methyl ethyl ketone, and other industrial solvents. In 2,3-butanediol (2,3-BD) biosynthesis, 2-acetolactate is formed after the condensation of two pyruvate molecules, and then it is converted into acetoin, which is subsequently reduced to yield 2,3-BD. After optimising the ribosomal binding sites of each gene, 2,3-butanediol (2,3-BD) production was improved (Oliver et al., 2013). A 1.8-fold increase in the production of 2,3-BD, when compared to the parent strain. Table 1 presents the list of chemical products produced by various cyanobacterial strains.

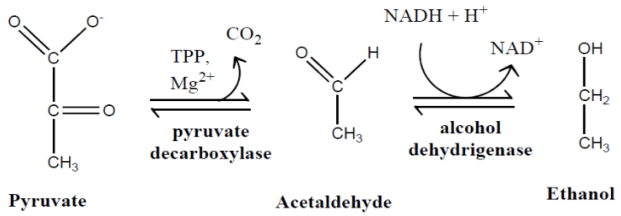

Fig 3. Metabolic Pathway of Pyruvate into Ethanol

Malonyl-CoA-derived product

The biodegradable precursor for the polymer is 3-hydroxypropionic acid (3-HP). In *Synechococcus elongatus* PCC7942, two 3-HP production pathways were constructed (Lan et al., 2015). The malonyl-CoA molecule is fragmented into malonate semialdehyde (MSA), which is subsequently reduced to 3-hydroxypropionaldehyde (3-HP), a process known as a malonyl-CoA-dependent pathway. Similarly, oxaloacetate is formed by the carboxylation of Phosphoenolpyruvate Carboxylase (PEP), which is used for the biosynthesis of amino acids via a metabolic pathway. Likewise, Aspartate was formed after transamination, and Alanine was formed after decarboxylation; it then undergoes a second

transamination reaction, transferring its amino group into α-ketoglutarate and forming glutamate. Within 16 days, a maximum of 3-hydroxypropionic acid was produced under independent β-alanine and malonyl-CoA pathways up to 186 mg/L (maximum productivity of 25 mg/L/d) and 659 mg/L (maximum productivity of 98 mg/L/d). *Synechocystis sp.* PCC6803 with both malonyl-CoA and β-alanine pathways produced 66 mg/L (maximum productivity; 102 mg/L/d) of 3HP at 16 days. The 3HP production rate was diminished twice due to malonyl-CoA within the pathway, as observed in *Chloroflexus aurantiacus* (Y. Wang et al., 2016).

Table 2. List of Cyanobacterial species for CO_2 tolerance capacity in %

Cyanobacteria	CO_2 tolerance capacity (%)	References
Scenedesmus sp., K34	80	Hanagata et al., 1992
Synechococcus elongatus	60	Miyairi 1995
Spirulina sp.,	12	De Morais and Costa 2007
Chlorella sp.,	9–10	Lee et al., 1996
Chlorococcum littorale	10–20	Lee at al., 1996
Botryococcus brauini	10	Yoo et al., 2010
Synechocystis aquatilis	5	Yoo et al., 2010
Dunatiella tertiolecta	10–20	Sydney et al., 2010
Monoraphidium minutum	2	Chiu et al., 2009

The gene-modified strains of cyanobacteria produce 689 mg/L of 3HP within 6 days. Production was generated by overexpressing pyridine nucleotide transhydrogenase genes, biotinylase, and endogenous acetyl-CoA carboxylase, which increased the NADH/NADPH ratio, ultimately resulting in 837 mg/L 3HP within 6 days. In 3HP, the biodegradable precursor for polymers is a mixture of isomers of hydroxybutyrate. The P_3HB_4HB (poly-3-hydroxybutyrate-co-4-hydroxybutyrate) is suitable for its flexible properties based on its composition (Ishida et al., 2001; Saito & Doi, 1994). Expressing heterologous of poly-3-hydroxybutyrate from *Chlorogleopsis fritschii* PCC9212 stimulates to form Poly(3-hydroxybutyrate-co-4-hydroxybutyrate) [P(3HB-co-4HB)] (S. Zhang et al., 2015). Cyanobacterial strains under the polyhydroxyalkanoate synthase (phaC) pathway produce Polyhydroxyalkanoates. Table 2 presents the list of Cyanobacterial species of CO_2 tolerance capacity (%).

High value-added natural products

Cyanobacteria utilise the 2-C-methyl-D-erythritol-4-phosphate (MEP) pathway for the production of terpenoids (Lange et al., 2000; M. Rohmer & Rohmer, 1999; M. S. M. H. S. B.-M. S. S. H. Rohmer, 1996). Terpenoids have numerous applications in consumer goods and industries due to their broad spectrum of structural diversity and varying molecular weights. Petroleum-based jet fuels, such as paraffin and kerosene, can be replaced with monoterpene (C10) compounds, which can in turn be replaced with diterpene (C20) compounds. Terpenes are used in the manufacturing of fuels, rubber, fragrances, flavors, and glues. Isoterpenes were produced from *Synechocystis* sp. PCC 6803 through a mevalonic acid (MVA) pathway (Bentley et al., 2014). Expression of the MVA pathway reverses the direction of the endogenous MEP pathway in *Synechocystis* sp. PCC 6803, into dimethylallyl diphosphate. Compared with other microbial strains, the MVA pathway of *Synechocystis sp*. PCC 6803 produced 2.4 times greater quantity of isoprene (Chaves et al., 2015). A cyclic monoterpene called limonene, a commercial product with various applications in pharmaceuticals, was produced from cyanobacterial strains (Chuck & Donnelly, 2014; Renninger, 2011). *Anabaena sp*. PCC7120, a potential filamentous cyanobacterial strain with nitrogen-fixing ability, can produce limonene (Halfmann et al., 2014). *Synechocystis sp.* PCC 6803 produces limonene at a concentration of up to 56 mg/L and is utilised in cosmetics, lubricants, and fragrances in commercial applications (Kiyota et al., 2014). Amyris biotechnology industry uses *Saccharomyces cerevisiae* for the biological production of farnesene. In this pathway, they provide sugar as a carbon source, which acts as a primary feedstock for the production of farnesene. After 15 days, *Anabaena* 7120 showed an extreme efficiency of 69 mg/L/OD700/d and a titer of 305 mg/L, producing high farnesene yield by overexpressing the farnesene synthase gene from Picea abies (Halfmann et al., 2014).

Fuel-like Isoprenoid and Bisabolene Products

Isoprenoid compounds are synthesized by methylerythritol phosphate (MEP) using encoded cyanobacteria. GAP and pyruvate are the starting routes for the MEP pathway. Most cyanobacteria utilize the MEP pathway to synthesize precursors for phytols, sterols, other pigments, and carotenoids (Lindberg et al., 2010). Due to the MEP Pathway in cyanobacteria, inherent control, and low natural carbon flow (Englund et al., 2015; Gao et al., 2016; X. Wang et al., 2016), high-yield isoprenoid compounds are produced (Englund et al., 2015). C10–C20 isoprenoid compounds are attractive as "green" reactor fuels because their

chemical properties are similar to those of petroleum-based fuels. Various C5–C30 compounds of isoprenoids are being prepared by integrating a single enzyme (Lindberg et al., 2010). Gao et al. (Gao et al., 2016) employed in silico modelling of cyanobacteria to stimulate flux and optimize carbon flow throughout the entire pathway, resulting in a significant increase in isoprene production. Complete route engineering is a method of overcoming the internal regulation of native routes that can limit a product's performance. For the production of larger isoprenoid compounds, terpene synthases have been introduced from plants to form intermediates of isoprenoids, such as caryophyllene, farnesene, β-phellandrene, squalene, bisabolene, and limonene (Bentley et al., 2014; Davies et al., 2014; Englund et al., 2014; Formighieri & Melis, 2015; Halfmann et al., 2014; Reinsvold et al., 2011). The commercial applications of bisabolene are cosmetics, pharmaceuticals, biofuels, nutraceuticals, and bioplastics. Engineered cyanobacteria 7002 species produce bisabolene and limonene *via* L-limonene synthase from Mentha spicata, and (E)-a-bisabolene synthase from Abies grandis produce 0.6 mg/L of a-bisabolene and 4 mg/L limonene (Englund et al., 2014). Squalene, a 30-carbon isoprenoid, is presently utilized in the production of vaccines and cosmetics. Large-scale production of squalene is used as a tremendous feedstock for biofuel production. It is produced naturally by several bacteria and serves as an intermediate in hopene biosynthesis, as well as the starting compound in hopanoid biosynthesis. Squalene–hopene cyclase, the enzyme capable of converting squalene into hopene. *Synechocystis sp.* PCC6803 genes of both squalene-hopene synthase (shc) and squalene synthase (sqs) are characterized and used for the production of squalene(Englund et al., 2014).

Cyanobacteria are capable of biosynthesizing a wide range of compounds, including carbohydrates, lipids, proteins, and secondary metabolites. Through genetic engineering and metabolic engineering approaches, researchers can modify cyanobacterial strains to optimize the production of specific chemicals and fuels (K. B. Singh et al., 2023; V. K. Singh et al., 2024). It opens up avenues for the sustainable synthesis of biofuels, pharmaceuticals, nutraceuticals, bioplastics, and other high-value compounds. By utilizing cyanobacteria as a feedstock, it becomes possible to reduce reliance on fossil fuels and petrochemicals while simultaneously mitigating CO_2 emissions. Cyanobacteria, as explained earlier in the article, also hold promise as a renewable source of biomass for biofuel production (Agarwal et al., 2022). Lipid-rich strains of cyanobacteria can be cultivated and harvested for lipid extraction, which can then be converted into biodiesel through transesterification processes.

Additionally, cyanobacteria can be engineered to produce bioethanol through fermentation pathways or to produce biohydrogen through photosynthetic processes. These biofuels offer environmentally friendly alternatives to conventional fossil fuels, with the potential to significantly reduce greenhouse gas emissions and enhance energy security. Despite the promising potential of CO_2-mitigating cyanobacterial species, several challenges must be addressed to fully realize their benefits in sustainable chemical and fuel production. However, it should be emphasized that these challenges also drive progress and the development of innovations in areas such as optimizing cultivation conditions, environmental impact and sustainability, genetic engineering and metabolic engineering, downstream processing, and economic viability. Large-scale cultivation of cyanobacteria may raise concerns about potential ecological consequences, including nutrient runoff, water consumption, and competition with natural ecosystems. Developing efficient cultivation systems and technologies to maintain optimal growth conditions can improve biomass productivity and overall efficiency (Quintana et al., 2011). Implementing sustainable cultivation practices, conducting life cycle assessments, and meeting regulatory requirements are crucial to ensuring the environmental sustainability of cyanobacterial-based production systems. While genetic engineering offers opportunities to enhance cyanobacterial strains for specific chemical production, it also presents challenges, including ensuring genetic stability, minimizing unintended effects, and optimizing metabolic pathways. Therefore, further research in the field of genetic and metabolic engineering is necessary (Zhang et al., 2017).

Efficient downstream processing techniques are crucial for extracting and purifying target chemicals and fuels from cyanobacterial biomass. Developing cost-effective and environmentally sustainable methods for biomass harvesting, cell disruption, and product recovery is essential to commercializing cyanobacterial-based processes. As observed during the research, Efficient downstream processing techniques are crucial for extracting and purifying target chemicals and fuels from cyanobacterial biomass. The development of cost-effective and environmentally sustainable methods for biomass collection, cell disruption, and product recovery, as well as addressing other challenges, is crucial for the commercialization of biotechnological processes involving cyanobacteria. Securing investment and cooperation between the research and scientific communities and industry are essential measures that

will enable increasing the scale of production and ensuring commercial success. Despite the challenges discussed, there are significant opportunities for innovation and growth in the field of CO_2-mitigating cyanobacterial species for sustainable chemical and fuel production. Advances in biotechnology, synthetic biology, and process engineering, combined with increasing awareness of environmental sustainability, create a favorable landscape for the development and adoption of cyanobacterial-based technologies. By addressing these challenges and seizing opportunities for collaboration and innovation, cyanobacteria can play a vital role in mitigating CO_2 emissions and advancing towards a more sustainable and resilient future.

Conclusion

This review provides a brief overview of the biological conversion of CO_2 into value-added products and their applications. CO_2-mitigating cyanobacterial species can produce isobutanol, isobutyraldehyde, 3-hydroxypropionic acid, poly(3HB), poly(3-HB-Co-4-HB), 2,3-butanediol, lactic acid, ethanol, mannitol, sucrose, glycogen, lysine, succinate, squalene, a-farnesene, a-bisaboline, and limonene. The metabolic pathways for every product were elaborated. Certain compounds, such as butanol, isobutanol, and ethanol, can be used as fuel in vehicles. Similarly, compounds such as 2,3-butanediol, lactic acid, and 3-hydroxypropionic acid can be used as bulk chemicals in the pharmaceutical industry. As a feedstock, cyanobacteria can absorb carbon dioxide and utilize it as a carbon source for growth regulation, as well as producing value-added products. These compounds have multiple applications in the medical, chemical, and food industries. To achieve a high yield of these compounds, at the industry level, engineered cyanobacterial species are now used. In the future, CO_2-tolerant cyanobacterial species will play a vital role in multidisciplinary research.

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Ethical approval

Not applicable

Conflict of Interest:

All authors declare that they have no conflict of interest.

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