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Review Article

A review of bioreactor configurations for hydrogen production by cyanobacteria and microalgae

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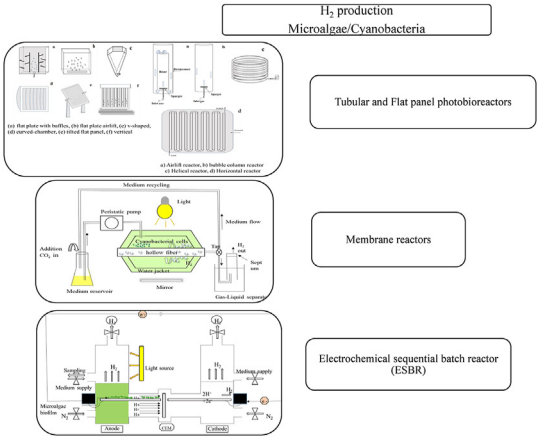
HIGHLIGHTS

- Review of biological production of hydrogen using microalgae and cyanobacteria.
- Source of C, N, P, micronutrients, light, temperature, gas, flow rate are discussed.
- Other strategies: S deprivation, anaerobic conditions, co-cultures, immobilization.
- Most common photobioreactors and novel systems with hydrogen yield.

GRAPHICAL ABSTRACT



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ABSTRACT

The need for cleaner energy as a sustainable alternative instead of fossil fuels has led to a plethora of research on biological H_2 production by microalgae and cyanobacteria. These species have a great potential to produce hydrogen in photobioreactors acting as a closed system that provides suitable conditions for algal cultivation. This review provides an overview of the requirements for green algae and cyanobacteria growth and focuses on the conditions required for hydrogen production. Also, the common types of bioreactors used

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for hydrogen production were critically assessed in terms of microbial growth and hydrogen production. Culturing these microorganisms within an electrochemical unit is a promising approach to increase biohydrogen production. The inclusion of nanoparticles is also an emerging technique to improve light scattering in photobioreactors.

Contents

1. Introduction

Globally, fossil fuels are the main source of energy but also the main contributor to global warming. Due to population growth, growing demand, and rising electricity costs, it becomes urgent to find alternative and more sustainable sources of energy. Hydrogen is a potential alternative with no CO_2 emissions associated with its combustion but has also a high energy of approximately 122 kJ g^{-1} [1]. Moreover, H_2 can be used in a wide range of applications such as outer space exploration, electricity generation in power plants, and many industrial processes (oil refineries, methanol production, etc.). It can also be used in hybrid energy systems (power storage) and vehicles [2,3]. These days, hydrogen has gained attention as a transportation fuel which has led to the manufacturing of electric vehicles. These vehicles include a tank of hydrogen that flows into fuel cells and reacts with oxygen from the air to produce electricity that powers an electric motor [3]. Among several methods to produce hydrogen like thermochemical, electrochemical, and biological processes, photobiological H_2 production by microalgae and cyanobacteria has received attention due to lower cost just by utilizing solar energy and CO_2 and converting them to biohydrogen [4] which was first reported by Gaffron in 1939 [5]. However, the amount of biological hydrogen production compared to other methods is very low due to hydrogenase and nitrogenase enzymes which are inhibited by oxygen.

To produce hydrogen using photosynthetic microorganisms, several photobioreactor (PBR) designs have been investigated: flat vs tubular panel, vertical vs horizontal bioreactors, and large-scale raceway pond design which have different geometric and hydrodynamic parameters that play an important role in light penetration, mixing regime and circulation required for optimum algal growth [1,6]. Hence, this review is focusing on the recent development of

photobioreactor design and process configuration and critically assesses their performance for biohydrogen production.

2. Microbial strains for H_2 production

2.1. Microalgae

Green algae can produce hydrogen through direct and indirect biophotolysis. In direct biophotolysis, they split water into H_2 and O_2 using sunlight. Microalgae containing chlorophyll *a* (Chl a) like plants can capture sunlight and use Photosystem I (PS I) and Photosystem II (PS II) pathways to produce oxygen through photosynthesis [7]. In PS II, solar energy is first absorbed to split protons (H^+), electrons (e^-), and O_2, and then electrons are transferred to PS I. In PS I, pigments absorb light energy which leads to an increase in the energy level of electrons to reduce ferredoxin oxidization; in the absence of O_2, the hydrogenase enzyme uses electrons from reduced ferredoxin (Fd) to convert H^+ to H_2 according to reactions 1 and 2 [7]:

$$2H_2O + h\upsilon \rightarrow O_2\uparrow + 4H^+ + Fd\ (red)\ (4e^-) \rightarrow Fd\ (red)\ (4e^-) + 4H^+ \rightarrow Fd\ (ox) + 2H_2 \quad (1)$$

$$H_2O—PSII—PSI—ferredoxin—hydrogenase—H_2 \quad (2)$$

The [Fe–Fe] hydrogenase enzyme has an efficiency of 12–14% when converting solar energy to H_2 and is also capable of oxidizing water to produce hydrogen. However, in indirect biophotolysis, energy for hydrogen production is supplied by endogenous carbohydrates stored in intracellular granules usually in the form of starch. To convert that stored energy in H_2 evolution, carbohydrates are fermented during dark conditions, and then hydrogenase enzyme transfer energy in the form of protons to form H_2 [7].

H_2 production by photosynthetic microorganisms (green algae) not only is dependent on environmental factors but also depends on the strain type [8]. Microalgae species including *Chlamydomonas reinhardtii*, *Tetraspora*, *Scenedesmus*, and *Chlorella* sp. [9–11] have the capability to produce hydrogen. Table 1 lists some of the most recent studies on H_2 production using microalgae and it can be seen that H_2 production was studied in small reactors (less than 500 mL) and well-controlled conditions (synthetic medium, temperature, gas atmosphere, mixing, light), but performance across studies is hard to compare because researchers used different units to report hydrogen volumes and produced yields. According to Supplementary Table A1, *C. reinhardtii* is the most studied strain and is able to produce the highest H_2 yield of 8.8 mL L^{-1} h^{-1} after 49 h when grown in a 500 mL cylindrical bottle photobioreactor (PBR) using tris-acetate-phosphate (TAP) medium at a temperature of 28–30 °C and light intensity of 40 μE m^{-2} s^{-1} [12] (Table 1). *Chlorella* species (*C. vulgaris*, *C. salina*, *C. lewinii*, *C. sorokiniana*, *C. pyrenoidosa*) have also demonstrated a good potential to produce hydrogen by the accumulation of a high amount of carbohydrates when they face nutrition deficiency [9,13] (Table 1). More recently, other strains such as *Ulothrix* and *Closterium* have been investigated for hydrogen production [14] (Table 1).

2.2. Cyanobacteria

The second group of microorganisms for hydrogen production are cyanobacteria which are divided into filamentous nitrogen-fixing and non-nitrogen-fixing blue-green algae which can both produce hydrogen through direct biophotolysis via nitrogenase or bidirectional hydrogenases enzymes as well as indirect biophotolysis [7,26].

The most common genera of filamentous nitrogen-fixing cyanobacteria are *Nostoc*, *Anabaena variabilis* ATCC 29,413, *Anabaena azollae*, *Synechocystis* sp. PCC6803, *Microcystis* PCC 7820, *Calothrix*, and *Oscillatoriaa* [27–30] (Table 2). These can produce hydrogen under nitrogen limitation via their nitrogenase enzyme which is located in heterocysts cells [8]. These cells are able to separate oxygen and hydrogen production by providing an environment free of oxygen for their nitrogenase enzymes which are sensitive to oxygen [7]. The H_2 production mechanism of filamentous nitrogen-fixing cyanobacteria is described by Eq. (3) as follows [31,32]:

$$N_2 + 8H^+ + 8e^- + 16ATP \rightarrow 2NH_3 + H_2 + 16ADP + 16P_i \quad (3)$$

In aerobic conditions (with nitrogen), filamentous nitrogen-fixing cyanobacteria consume ATP, fix N_2 and convert it to NH_3 and generate H_2 as a byproduct [7]. Yodsang et al. (2018) also reported that some filamentous nitrogen-fixing cyanobacteria have the potential to produce hydrogen under an argon atmosphere as shown in Table 2 [33].

However, in non-heterocystous cyanobacteria, the bidirectional hydrogenase enzyme pathway is dominant when producing hydrogen under anaerobic conditions (without nitrogen) [34]. The commonly used non-nitrogen-fixing genera of cyanobacteria include *Gloebacter* PCC7421(a unicellular cyanobacterium), *Synechococcus*, and *Aphanocapsa montana* [7,35]. Eq. (4) describes the mechanism of H_2 production in non-nitrogen-fixing cyanobacteria.

$$8H^+ + 8e^- + 16ATP \rightarrow 4H_2 + 16ADP + 16P_i \quad (4)$$

For example, H_2 production from non-heterocystous cyanobacterium *Gloebacter* PCC7421 under an atmosphere of Ar, CO, and C_2H_2 and light intensity of 30 μE m^{-2} s^{-1} was 1.38 μmol h^{-1} g^{-1} (Chl) [36] (Table 2). Also, the filamentous non-heterocystous cyanobacterium *Geitlerinema* sp. RMK-SH10 has recently shown a capability of H_2 production [37] (Table 2). However, these strains cannot rival the yield achieved by *Anabaena* sp.

To produce H_2 via indirect biophotolysis, cyanobacteria use the stored energy from endogenous carbohydrates (glycogen). A non-nitrogen-fixing cyanobacterium *Gloeocapsa alpicola* CALU743 is a good example which demonstrated high performance of H_2 production 20 mL L^{-1}_{matrix} h^{-1} during indirect biophotolysis [38] (Table 2).

Several recent studies on the production of H_2 by cyanobacteria are listed in Table 2 and it can be seen that nitrogen-fixing cyanobacteria such as *Anabaena* PCC 7120, which produced 1600 mL L^{-1} hydrogen under N_2 atmosphere and darkness, are more promising to produce H_2 [39].

Table 1 – H_2 production rate by various microalgae.

Microalgae	Growth conditions	H_2 production conditions	H_2 production	Reference
Chlamydomonas reinhardtii wt 137c	tris-acetate-phosphate medium (TAP), pH 7.2, 25 °C, 110 μE m^{-2} s^{-1}	sulfur-deprived medium (TAP-S), 25 °C, 110 μE m^{-2} s^{-1}, under N_2 bubbling, a torus-shaped photobioreactor	2.5 mL L^{-1} h^{-1}	[15]
Chlamydomonas reinhardtii Dangeard C137+	tris-acetate-phosphate (TAP) medium, pH 6.9, 28 °C, 100 μE m^{-2} s^{-1}, 500- mL flasks bottles	sulfur-free TAP medium (TAP-S), 28 °C, 100 μE m^{-2} s^{-1}, 14 –14.5 mL vials	2.8–2.9 mL L^{-1} h^{-1}	[16]
Chlorella sorokiniana Ce	tris-acetate-phosphate (TAP) medium, 120 μE m^{-2} s^{-1}, pH 7.2, 30 °C	sulfur-free TAP medium (TAP-S), 120 μE m^{-2} s^{-1}, pH 7.2, 30 °C, batch mode, 500 mL flasks bottles	1.35 mL L^{-1} h^{-1}	[17]
Chlorella vulgaris	Artificial wastewater medium, immobilized, 140 μE m^{-2} s^{-1}, 25 ± 1 °C	Wastewater medium + 10 g L^{-1} glucose + sulfur deprivation, 140 μE m^{-2} s^{-1}, purple light, 25 ± 1 °C, under N_2 atmosphere, pH 8	1.63 mL L^{-1} h^{-1} (or 39.18 mL L^{-1} day^{-1})	[18]
Scenedesmus obliquus	Artificial wastewater medium, immobilized, 140 μE m^{-2} s^{-1}, 25 ± 1 °C	Wastewater medium + 10 g L^{-1} glucose + sulfur deprivation, 140 μE m^{-2} s^{-1}, purple light, 25 ± 1 °C, under N_2 atmosphere, pH 8	8.53 mL L^{-1} h^{-1} (or 204.8 mL L^{-1} day^{-1})	[18]
Chlorella Salina Mt	tris-acetate-phosphate (TAP) medium, 30 °C, 120 μE m^{-2} s^{-1}, pH 7.2	sulfur-free TAP medium (TAP-S), 30 °C, 120 μE m^{-2} s^{-1}, pH 7.2, 500 mL flasks	0.5 mL L^{-1} h^{-1}	[17]
Chlorella sorokiniana KU204	tris-acetate-phosphate (TAP) medium + 0.7 mM N_4Cl, 25 °C, 35 μE m^{-2} s^{-1}, 14:10 h light/dark cycle, pH 7.3	sulfur-free TAP medium (TAP-S) + 0.7 mM NH_4Cl, 25 °C, 35 μE m^{-2} s^{-1}, pH 7.3, under Ar, 650 mL bioreactors	Maximum H_2 1.30 mL L^{-1} h^{-1} And total H_2 89.64 mL L^{-1}	[13]
Chlorella sp. KU209	tris-acetate-phosphate (TAP) medium + 0.7 mM N_4Cl, 25 °C, 35 μE m^{-2} s^{-1}, 14:10 h light/dark cycle, pH 7.3	sulfur-free TAP medium (TAP-S) + 0.7 mM NH_4Cl, 25 °C, 35 μE m^{-2} s^{-1}, pH 7.3, under Ar, 650 mL bioreactors	12.67 mL L^{-1}	[13]
Chlorella lewinii KU201	tris-acetate-phosphate (TAP) medium + 0.7 mM N_4Cl, 25 °C, 35 μE m^{-2} s^{-1}, 14:10 h light/dark cycle, pH 7.3	sulfur-free TAP medium (TAP-S) + 0.7 mM NH_4Cl, 25 °C, 35 μE m^{-2} s^{-1}, pH 7.3, under Ar, 650 mL bioreactors	13.03 mL L^{-1}	[13]
Chlamydomonas reinhardtii Dangeard C137+	tris-acetate-phosphate (TAP) medium, 28–30 °C, 20 –40 μE m^{-2} s^{-1}	sulfur-free TAP medium (TAP-S), at 30 mg L^{-1} chl, 52 μE m^{-2} s^{-1}, under argon (Ar), in 500 mL cylindrical bottles or at light intensity 40 μE m^{-2} s^{-1}	175 mL L^{-1} 8.8 mL L^{-1} h^{-1} after 49 h	[12]
Chlamydomonas reinhardtii CC1036 pf18 mt+	immobilized on fiber glass, tris-acetate-phosphate (TAP) medium, 120 μE m^{-2} s^{-1}, 27–29 °C	sulfur-free TAP medium (TAP-S), at 6 mL L^{-1} flow rate of TAP medium, 120 μE m^{-2} s^{-1}, under argon (Ar), using rectangular PBR (160 mL volume)	2375 mL L^{-1} $_{PBR}$ over 23 days	[19]
Chlamydomonas reinhardtii CC1036 pf18 mt+	immobilized on fiber glass, tris-acetate-phosphate (TAP) medium, 120 μE m^{-2} s^{-1}, 27–29 °C	a steady flow rate of TAP medium with 10–20 μM sulfate, under argon (Ar), rectangular PBR (160 mL volume)	2812 mL L^{-1} $_{PBR}$ for 90 days	[20]
Chlorella vulgaris NIER-10003	MA medium, 95% air + 5% CO_2, pH 8.0, 120 μE m^{-2} s^{-1}, 25 °C	sulfur-deprived (MA-S) medium, cylindrical, conical ended photobioreactor (1 L)	809 ± 10 mL L^{-1}	[21]
Chlorella protothecoides	TAP medium, pH 7.3 ± 1, 25 ± 1 °C, 30–35 μE m^{-2} s^{-1}, 14 h:10 h light-dark cycle	TAP medium by N-limited combined with sulfur-deprived (LNS), 30–40 μE m^{-2} s^{-1} after 24 h, Glass tubes (16.5 mL)	140.4 mL L^{-1}	[22]
Chlorella pyrenoidosa	Tris-Acetate-Phosphate (TAP) medium + 10 mM $NaHCO_3$ (TCP medium), immobilized, pH 7, 180 ± 10 μE m^{-2} s^{-1}, 28 °C, a 3.925- L airlift PBR	TCP medium + injection of 10 μM DCMU (3-(3,4-dichlorophenyl)-1,1-dimethylurea), after 9 h injection, under N_2, under 24 h darkness then 180 ± 10 μE m^{-2} s^{-1}, 28 °C, anaerobic bottles with 75 mL TCP medium	93.86 mL L^{-1}	[23]
Tetraspora sp. CU2551	Tris-Acetate-Phosphate (TAP) medium, immobilized, pH 7.2, 29 μE m^{-2} s^{-1}, 36 °C, 125-mL Erlenmeyer flasks	sulfur-free TAP medium (TAP-S), under air, pH 7.2, 29 μE m^{-2} s^{-1}, 36 °C, 100-mL gas-tight vials	0.182 ± 0.020 μmol h^{-1} mg^{-1} dry wt	[24]
Tetraspora sp. CU2551	Tris-Acetate-Phosphate (TAP) medium, immobilized, pH 7.2, 29 μE m^{-2} s^{-1}, 36 °C, 125-mL Erlenmeyer flasks	sulfur-free TAP medium (TAP-S), under Ar, pH 7.2, 29 μE m^{-2} s^{-1}, 36 °C, 100-mL gas-tight vials	1.182 ± 0.024 μmol h^{-1} mg^{-1} dry wt	[25]
Closterium moniliferum AARL G041	Jaworski's medium (JM), autotrophically, 30.8 μE m^{-2} s^{-1}, 25 °C	sulfur-free JM medium (JM-S), 54 μE m^{-2} s^{-1}, 25 °C, under Ar, 60 mL vial serum bottles	0.38 μmol h^{-1} mg^{-1} (Chl)	[14]
Chlorella sp. AARL G014	Tris-Acetate-Phosphate (TAP) medium, mixotrophically, 30.8 μE m^{-2} s^{-1}, 25 °C	sulfur-free TAP medium (TAP-S), 54 μE m^{-2} s^{-1}, 25 °C, under Ar, 60 mL vial serum bottles	0.49 μmol h^{-1} mg^{-1} (Chl)	[14]
Ulothrix cf. *tenerrima* AARL G029	Tris-Acetate-Phosphate (TAP) medium, 30.8 μE m^{-2} s^{-1}, 25 °C	sulfur-free TAP medium (TAP-S), 54 μE m^{-2} s^{-1}, 25 °C, under Ar, 60 mL vial serum bottles	0.31 μmol h^{-1} mg^{-1} (Chl)	[14]

Table 2 – H_2 production rate by various cyanobacteria.

Cyanobacteria	Growth conditions	H_2 production condition	H_2 production rate	References
Anabaena variabilis PK84	Allen and Arnon medium, air +2% CO_2, sunlight	Allen and Arnon medium, air +2% CO_2, sunlight, batch mode, during 40 days, 4.35 L- outdoor tubular PBR	45.8 mL h^{-1} (or total H_2 of 24.5 L)	[40]
Anabaena sp. PCC 7120 ΔHup	8 times-diluted Allen–Arnon medium (AA/8), 30 μE m^{-2} s^{-1}, 27 °C, 99% air + 1% CO_2	8 times-diluted Allen–Arnon medium without nitrogen (AA/8-N) medium, 290 and 340 μE m^{-2} s^{-1}, Ar with 5% CO_2, and 3.3% N_2, pH 8.2, 22 °C, Plastic bags (1 L)	0.86 mL h^{-1} L^{-1} or 20.6 mL day^{-1} L^{-1} or 33.2 mL L^{-1} during 5 days	[41]
Anabaena variabilis PK84	Nitrogen-free BG11 medium ($BG11_0$ medium) + Na_3VO_4, 80 μE m^{-2} s^{-1}, 99% air + 1% CO_2, 30 °C	$BG11_0$ medium + Na_3VO_4, 353 μE m^{-2} s^{-1}, under 99% Ar + 1% CO_2, pH 7 ± 0.05, 36 °C, a 1.25 L-three coaxial glass cylinders PBR	20 mL L^{-1} h^{-1}	[42]
Gloeocapsa alpicola CALU 743[a]	First stage: BG11 medium + 1.5 μM $NiCl_2$, 165 μE m^{-2} s^{-1}, temperature 30 °C, 98% air + 2% CO_2, immobilized in a glass fiber, second stage: in a 160 mL rectangular PBR + immobilized in a glass fiber, a mixture of 98% air + 2% CO_2, 28 °C, 72 μE m^{-2} s^{-1}	Nitrogen-free BG11 medium ($BG11_0$ medium) + 1.5 μM $NiCl_2$ +10 mM HEPES, pH 7.5, under dark and Ar atmosphere, a 160 mL rectangular PBR	20 mL L^{-1}_{matrix} h^{-1}	[38]
Anabaena PCC 7120	Nitrogen-free BG11 medium ($BG11_0$ medium, thermophilic mixed culture, 120 μE m^{-2} s^{-1}, a 1.4 L airlift PBR	replacing glucose with 1% (w/v) pretreated algal biomass with amylase, batch mode, thermophilic condition, for 24 h, under N_2 atmosphere, pH 5.5, a 500 mL double jacketed bioreactor	1600 mL L^{-1}	[39]
Immobilized Synechocystis sp. PCC 6803[a]	BG11 medium, 28 °C, 70 μE m^{-2} s^{-1}, 97% air +3% CO_2, Glass tube (400 mL)	nitrogen-free medium $BG11_0$ -Tris, 60 μE m^{-2} s^{-1}, 28 °C, under N_2 atmosphere, serum vials (60 mL)	Total H_2 5.80 ± 0.14 mL Or maximum H_2 5.73 ± 0.69 mL mg $cells^{-1}$	[30]
Nostoc linckia HA-46	BG-11 medium, light intensity 3000 lx (Lux), 28 ± 3 °C	BG-11 medium, 18 h: 6 h light-dark cycle, pH 8.0, 31 °C, CO_2:Ar ratio 2:10, after 24 h, 15-mL vials	93–105 μmol h^{-1} mg^{-1} (Chl)	[43]
Calothrix elenkinii	BG11 medium, pH 7.5, bubbling with air, 50 μE m^{-2} s^{-1}, 30 °C	Nitrate-free BG11 medium ($BG11_0$ medium) + 0.3% glucose, under Ar, optimal pH 7.5, 25 °C, 250 μE m^{-2} s^{-1}, a 20-mL vial	0.09 ± 0.01 μmol mg^{-1}(Chl) h^{-1}	[33]
Fischerella muscicola	BG11 medium, pH 7.5, bubbling with air, 50 μE m^{-2} s^{-1}, 30 °C	Sulfur and nitrogen-free BG11 medium ($BG11_0$-s medium) + 0.1% glucose, under Ar, optimal pH 7.5, temperature 25 °C, 250 μE m^{-2} s^{-1}, a 20- mL vial	0.35 ± 0.08 μmol mg^{-1}(Chl) h^{-1}	[33]
Nostoc calcicola	BG11 medium, pH 7.5, bubbling with air, 50 μE m^{-2} s^{-1}, 30 °C	Nitrate-free BG11 medium ($BG11_0$ medium)+ 0.1% glucose, under Ar, optimal pH 7.5, 25 °C, 250 μE m^{-2} s^{-1}, a 20- mL vial	0.09 ± 0.01 μmol mg^{-1}(Chl) h^{-1}	[33]
Scytonema bohneri	BG11 medium, pH 7.5, bubbling with air, 50 μE m^{-2} s^{-1}, 30 °C	Nitrate-free BG11 medium ($BG11_0$ medium)+ 0.3% glucose, under Ar, optimal pH 7.5, 25 °C, 250 μE m^{-2} s^{-1}, a 20- mL vial	0.09 ± 0.01 μmol mg^{-1}(Chl) h^{-1}	[33]
Tolypothrix distorta	BG11 medium, pH 7.5, bubbling with air, 50 μE m^{-2} s^{-1}, 30 °C	Nitrate-free BG11 medium ($BG11_0$ medium) + 0.1% glucose, under Ar, optimal pH 7.5, 25 °C, 250 μE m^{-2} s^{-1}, a 20- mL vial	0.21 ± 0.05 μmol mg^{-1}(Chl) h^{-1}	[33]
Gloebacter PCC7421[a]	BG11 medium, pH 7, bubbling with air, 20 μE m^{-2} s^{-1}, 25–30 °C	under Ar, 30 μE m^{-2} s^{-1}, 7.8 mL gas-tight bottles	1.38 μmol mg^{-1}(Chl) h^{-1}	[36]
Nostoc muscorum	Arnon's (AA) medium with KNO_3, 30 ± 1 °C, 16 h: 8 h light-dark cycle, light intensity 3 klx (Kilolux)	nitrogen-free AA-N medium + glucose, 40 °C, after 24 h, under light and Ar, 13-mL vials	0.046 μmol h^{-1} mg^{-1} dry mass	[44]
Leptolyngbya valderiana BDU20041	ASN III medium, light intensity 13.7 W m^{-2}, 27 ± 2 °C	Nitrogen-free ASN III–N medium, 27 ± 2 °C, after 24 h, under dark and Ar atmosphere	0.019 μmol h^{-1} mg^{-1} dry wt	[45]
Plectonema terebrans BDU141311	ASN III medium, light intensity 13.7 W m^{-2}, 27 ± 2 °C	Nitrogen-free ASN III–N medium, 27 ± 2 °C, after 24 h, under light and N_2 atmosphere	0.013 μmol h^{-1} mg^{-1} dry wt	[45]

Plectonema terebrans BDU30343	ASN III medium, light intensity 13.7 W m^{-2}, 27 ± 2 °C	Nitrogen-free ASN III–N medium, 27 ± 2 °C, after 24 h, under dark and N_2 atmosphere	0.015 μmol h^{-1} mg^{-1} dry wt	[45]
Lyngbya confervoides BDU142001	ASN III medium, light intensity 13.7 W m^{-2}, 27 ± 2 °C	Nitrogen-free ASN III–N medium, 27 ± 2 °C, after 24 h, under dark and N_2 atmosphere	0.021 μmol h^{-1} mg^{-1} dry wt	[45]
Lyngbya confervoides BDU140301	ASN III medium, light intensity 13.7 W m^{-2}, 27 ± 2 °C	Nitrogen-free ASN III–N medium, temperature 27 ± 2 °C, after 24 h, under dark and Ar atmosphere	0.013 μmol h^{-1} mg^{-1} dry wt	[45]
Microcoleus chthnoplasts BDU91212	ASN III medium, light intensity 13.7 W m^{-2}, 27 ± 2 °C	Nitrogen-free ASN III–N medium, temperature 27 ± 2 °C, after 24 h, under light and Ar atmosphere,	0.017 μmol h^{-1} mg^{-1} dry wt	[45]
Geitlerinema sp. RMK-SH10	ASN III medium, 30 μE m^{-2} s^{-1}, 30 °C	Nitrogen-free ASN III–N medium +0.2 M NaCl +18.9 mmol C-atom L^{-1} glucose +0.1 μM Ni^{2+}, 30 °C, under dark and Ar atmosphere, a 10-mL gas-tight vial	0.271 μmol h^{-1} mg^{-1} dry wt	[37]
Gloeocapsa alpicola CALU 743=(*Synechocystis* PCC 6308)[a]	$BG11_0$ medium, 165 μE m^{-2} s^{-1}, 98% air + 2% CO_2, 30 °C	$BG11_0$ medium, under dark and Ar atmosphere, optimal pH 6.8–8.3, 40 °C, 40-mL bottles	25 μL h^{-1} mg^{-1} dry wt	[46]
Oscillatoria sp. Miami BG7	medium A, Nitrogen-free medium A-N, and combined nitrogen-limited medium, 30 W, 25 °C	combined nitrogen-limited medium with 5 mL g^{-1} KNO_3, pH 7.0, under Ar, 30 μE m^{-2} s^{-1}, 25 °C, a 15 mL glass flask	6.4 μL h^{-1} mg^{-1} dry wt = (260 μmol mg^{-1}(Chl) h^{-1})	[47]
Anabaena variabilis ATCC 29413	Allen–Arnon medium, 65 ± 2 μE m^{-2} s^{-1}, 95% air + 5% CO_2, 30 °C	Allen–Arnon medium, under Ar atmosphere, 150 ± 5 μE m^{-2} s^{-1}, A flat panel PBR	7.73 mL g^{-1} dry cell h^{-1}	[27]

[a] = is unicellular strain.

3. Macro and micronutrients

Microalgae culture medium can be considered as an artificial and sterile environment in which microorganisms are able to grow and reproduce. Such environments must provide four main components, i.e. nutrients, rare elements, water, and carbon dioxide for optimal microalgae growth. For example, hydrogen production by *Synechocystis* sp. PCC 6803 increased 150 folds when key nutrients were optimized in the culture medium [48]. Carbon, nitrogen, hydrogen, and oxygen are the most important macronutrients for algal and cyanobacterial growth and are listed with micronutrients in Table 4 [49].

3.1. *Source of C*

Carbon source not only is an essential and major substance for algal growth and H_2 production but also the yield of biomass and hydrogen production varies depending on the type and amount of this element [50]. Carbon can exist either in the inorganic (CO_2) or organic form (glucose, mannitol, acetate, sucrose, …) which algae species consume for their growth and convert to starch and glycogen which is used in anaerobic conditions [51]. However, the amount of starch and glycogen storage by microalgae is restricted which leads to a low level of H_2 production, especially when they utilize CO_2 as their carbon source (in autotrophic conditions); hence, to increase the rate of hydrogen production, exogenic carbon sources have been supplied like glucose, fructose, sucrose, malt extract, malic acid, acetate, and organic wastewater [52]. Table 3 shows a comparison of H_2 production under heterotrophic and autotrophic conditions. In heterotrophic conditions (organic carbon source), microalgae can produce more hydrogen than under autotrophic conditions. Moreover, hydrogen production under heterotrophic conditions can be more economical when less expensive carbon sources (organic wastes) are used and when there is no need for an artificial light source [50]. Researchers studied different organic carbon sources such as malic acid, butyric acid, acetic acid, potato starch, cellulose, corn starch, fructose, sucrose, and malt extract to evaluate the possibility of H_2 production from these resources. Only glucose, fructose, sucrose, and malt extract were found to be suitable for hydrogen production with an average rate of 8, 24, 18 and 19 mL L^{-1} h^{-1} and maximum volume of 812 ± 5, 874 ± 5, 1315 ± 5, and 1144 ± 5 mL L^{-1}, respectively (Table 3). They also found that the optimum concentration of each carbon source was 5 g L^{-1} and above this value, the amount of H_2 production decreased [21]. Another work investigated the impact of glucose, sucrose, fructose, and malt extract as carbon sources on hydrogen production by *Microcystis aeruginosa* [53]. A maximum hydrogen yield of 1243 ± 3 mL L^{-1} and an average rate of 21.05 mL L^{-1} h^{-1} was produced using malt extract (Table 3). Chen et al. (2008) also observed that using 200 mg L^{-1} fructose and sucrose as a substrate for *Anabaena* sp. CH_3, it was able to produce 0.0016 and 0.001 mol of hydrogen, respectively [54]. Some studies investigated the effect of acetate on H_2 production. For example, Laurinavichene et al. (2006) emphasized the importance of using acetate for hydrogen production from sulfur-deprived *C. reinhardtii*. They

Table 3 – Different carbon sources for H_2 production by various microalgae and cyanobacteria.

Microorganism	Substrate	H_2 production rate	Reference
Chlamydomonas reinhardtii	Acetate	2.1 mL L^{-1}_{cult} h^{-1}	[19]
Chlorella vulgaris	Glucose (5 g L^{-1})	8 mL L^{-1} h^{-1}	[21]
	Fructose (5 g L^{-1})	24 mL L^{-1} h^{-1}	
	Sucrose (5 g L^{-1})	18 mL L^{-1} h^{-1}	
	Malt extract (5 g L^{-1})	19 mL L^{-1} h^{-1}	
Microcystis aeruginosa	Glucose (5 g L^{-1})	3.07 mL L^{-1} h^{-1}	[53]
	Fructose (5 g L^{-1})	10.1 mL L^{-1} h^{-1}	
	Sucrose (5 g L^{-1})	12.5 mL L^{-1} h^{-1}	
	Malt extract (5 g L^{-1})	21.05 mL L^{-1} h^{-1}	
Chlamydomonas reinhardtii	(2% CO_2 + Acetate)	1.67 mL L^{-1} h^{-1}	[56]
	2% CO_2	0.31 ± 16.7 mL L^{-1} h^{-1}	[60]
	Acetate	1.43 mL L^{-1} h^{-1} in synchronized culture	[61]
	Acetate	1.14 mL L^{-1} h^{-1} in unsynchronized culture	[61]
Chlorella sorokiniana Ce	Acetate	1.35 mL L^{-1}_{cult} h^{-1}	[17]
Calothrix elenkinii	0.3% (w/v) Glucose	3.21 ± 0.19 μmol mg^{-1} (Chl) h^{-1}	[33]
Fischerella muscicola	0.1% (w/v) Glucose	8.73 ± 0.43 μmol mg^{-1} (Chl) h^{-1}	
Scytonema bohneri	0.3% (w/v) Glucose	7.63 ± 0.26 μmol mg^{-1} (Chl) h^{-1}	
Nostoc calcicola	0.1% (w/v) Glucose	4.27 ± 0.17 μmol mg^{-1} (Chl) h^{-1}	
Tolypothrix distorta	0.1% (w/v) Glucose	10.95 ± 0.22 μmol mg^{-1} (Chl) h^{-1}	
Synechocystis sp. PCC 6803	0.1% Glucose	0.12 ± 0.02 μmol mg^{-1} (Chl) h^{-1}	[62]
Oscillotoria limosa	0.5% (w/v) Glucose	34.5 μmol mg^{-1} (Chl) h^{-1}	[63]
Synechocystis sp. PCC 6803	$NaHCO_3$	0.81 ± 0.36 μmol mg^{-1} (Chl) h^{-1}	[48]
Anabaena siamensis TISTR 8012	0.5% Fructose	31.79 μmol mg^{-1} (Chl) h^{-1}	[64]
	CO_2	15.2 μmol mg^{-1} (Chl) h^{-1}	
Cyanothece sp. ATCC 51142	Glycerol	3.729 mL g^{-1} h^{-1}	[65]
Chlamydomonas MGA 161	5% CO_2	0.97 ± 0.21 μmol mg^{-1} dry wt $(6\ h)^{-1}$	[66]
Anabaena cylindrica B 629	3% CO_2	0.103 μmol mg^{-1} dry wt h^{-1}	[67]
Anabaena variabilis ATCC 29413	5% CO_2	7.73 mL g^{-1} dry cell h^{-1}	[27]
Anabaena azollae	2% CO_2	13 mL L^{-1}_{cult} h^{-1}	[28]
Chroococcidiopsis thermalis CALU 758	1% CO_2	0.7 μmol mg^{-1} (Chl) h^{-1}	[68]
Anabaena PCC 7120	1% CO_2	8 μmol mg^{-1} (Chl) h^{-1}	[69]
Chlamydomonas reinhardtii CC124	3% CO_2	0.32 mL L^{-1} h^{-1}	[70]
Anabaena variabilis ATCC 29413	5% CO_2	31 μmol mg^{-1} (Chl) h^{-1}	[71]
Gloeocapsa alpicola CALU 743	4% CO_2	0.14 μmol mg $protein^{-1}$ h^{-1}	[72]
Anabaena variabilis AVM13	1% CO_2	68 μmol mg^{-1} (Chl) h^{-1}	[73]
Anabaena variabilis PK84	2% CO_2	80 mL h^{-1}	[74]

Table 4 – Typical elemental composition of algal biomass; adapted from Ref. [49].

Element	Mass per dry weight of microalgae (μg mg^{-1})	Element	Mass per dry weight of microalgae (μg mg^{-1})
Carbon	175–650	Potassium	1–75
Oxygen	205–330	Phosphorus	0.5–33
Hydrogen	29–100	Magnesium	0.5–75
Nitrogen	10–140	Sodium	0.4–47
Calcium	0–80	Iron	0.2–34
Sulfur	1.5–16	Boron	0.001–0.25
Zinc	0.005–1.0	Copper	0.006–0.3
Manganese	0.02–0.24	Molybdenum	0.0002–0.001
Silica	0–230	Cobalt	0.0001–0.2

observed that in the absence of acetate no hydrogen was produced, while adding 16.7 mM acetate led to a total H_2 production of 300 mL [19]. Another work also showed that 17 mM acetate in the culture medium was necessary for H_2 production from sulfur-deprived *C. reinhardtii*. A rapid increase in hydrogen production rate of 0.24 mL L^{-1} h^{-1} and complete consumption of acetate was then followed by a sudden decrease in bioH_2 production [55]. Kosourov et al. (2007) also studied H_2 production by sulfur-deprived *C. reinhardtii* under photomixotrophic condition. They found that in order to produce a maximum hydrogen yield of 4.5 ± 1.6 mmol L^{-1} or 100 mL L^{-1}, both acetate (17.4 mM) and CO_2 (2%) were essential (Table 3) [56]. In a different study using wastewater as a culture medium, the impact of different acetate/Cl^- ratios on hydrogen production from *C. reinhardtii* and *C. sorokiniana* were investigated. At a constant Cl^- concentration of 17 mM, an optimal concentration of acetate was found to be 25 mM which resulted in a H_2 production rate of 15–19.8 μmol L^{-1} h^{-1} for *C. sorokiniana* and 12–22.8 μmol L^{-1} h^{-1} for *C. reinhardtii* [57]. However, Skjanes et al. (2007) suggested using CO_2 emission from industries because carbon dioxide is cheaper, and the process can

sequester CO_2 from the atmosphere [58]. Marques et al. (2011) also studied the inclusion of 1% CO_2 in the gas phase of glass bottles with a 30 mL culture of *Anabaena* sp. PCC 7120 and its mutants (hupL$^-$ and hupL$^-$/hoxH$^-$). They observed that the highest H_2 production rate of 62.6 and 54.8 μmol H_2 mg^{-1} (Chl a) h^{-1} was achieved by hupL$^-$ and hupL$^-$/hoxH$^-$, respectively [59].

3.2. Nitrogen

Nitrogen which is the second most important element for algal and cyanobacterial growth constitutes 7% of algal dry weight (wt). To prepare a culture medium, nitrogen can be sourced from an organic (e.g. urea) or inorganic form (nitrate NO_3^-, ammonium NH_4^+) [75]. As nitrogen plays an important role in microalgal metabolic pathways, an increase in nitrogen concentration in the medium produces more cells. It was reported that adding nitrate during fed-batch culture led to an increase of 56.6% and 68.8% CO_2 uptake rate for microalgae and cyanobacteria, respectively because the exponential growth phase expanded for more than 3 days [76]. On the other hand, a deficiency of this nutrient leads to a significant increase in lipid storage and a restriction in photosynthesis [77]. The source of nitrogen such as nitrogen-ammonia, glutamate, or yeast extract influences hydrogen production due to the inhibition of the nitrogenase enzyme in cyanobacteria by ammonia [78]. A 4-fold increase in H_2 production was observed by *C. elenkinii, F. muscicola, N. calcicola, S. bohneri, T. distorta* when they were cultivated in a medium without nitrate [33]. Researchers also reported that by transferring *Aphanothece halophytica* from BG-11 medium with 17 mM $NaNO_3$ to a nitrate-free medium the rate of hydrogen production increased from about 0.4 to 1.617 ± 0.187 μmol H_2 mg^{-1} (Chl a) h^{-1} [79]. However, it was reported that an immobilized cyanobacterial species like *A. variabilis* ATCC 29413 could produce up to 67 mL h^{-1} L^{-1} after 2 months in a contaminated medium with ammonium if it is cultivated in a photobioreactor [80].

Dinitrogen gas (N_2) (in the headspace of PBR) can also inhibit hydrogen production by cyanobacteria. In the presence of N_2, around 75% of ATP and electrons that are transferred to the active site of the molybdenum-nitrogenase, are available for hydrogen production, while in the N_2-free atmosphere all electrons and ATP transferred are used for bioH_2 production [81]. To evaluate the effect of dinitrogen gas on hydrogen production, Yeager et al. (2011) used different N_2 atmospheres with argon (<1, 5, 20, or 80%) for *Anabaena cylindrica* B629, *Tolypothrix* sp. B379, *Anabaena* sp. PCC 7120, *Fischerella muscicola* PCC 7414, *Nostoc commune* MFG-1, *Scytonema hylanium* NCC-4B, *Calothrix* sp. MCC-3, and *Fischerella* sp. Dx-SRS. They found that all strains were able to produce the greatest volumes of hydrogen in <1% N_2 concentration of the headspace, but hydrogen volumes under 5, 20, and 80% N_2 were less than 38–61%, 71–92%, and 89–97%, respectively in comparison with <1% N_2 [81]. Other researchers also claimed that in the presence of a high amount of dinitrogen gas, *Anabaena* sp. PCC 7120 could only produce a small amount of hydrogen [82]. Another study confirmed that *A. variabilis* produced a low volume H_2 under 93% Ar, 5% N_2, and 2% CO_2 atmosphere [83].

3.3. Sulfur

Sulfur is another important element for algal growth and hydrogen production. Most studies have evaluated the effect of sulfur deprivation on H_2 production by causing stress conditions leading to an accumulation of carbohydrate and lipids in algal cells which in turn are consumed by cells to produce biohydrogen [84]. As sulfur deprivation restricts photosynthesis activity, restrains O_2 evolution, reduces carbon sequestration, and increases starch and lipids catabolism, it provides favorable conditions for hydrogen production. Sulfur deprivation is affected by light and cultivation conditions that results in a variation in bioH_2 production [50,85]. The impact of light on sulfur deprivation is discussed in more details in another paragraph dedicated to the light effect. Regarding cultivation conditions, the concentration of CO_2 influences anaerobiosis in sulfur deprivation. For example, if microalgae grow in a medium with a high CO_2 concentration, early anaerobiosis is attained due to consumption of all sulfur by cells which leads to anaerobic conditions and more H_2 production. Anaerobiosis also depends on growth phase, for example, early anaerobiosis is achieved when microalgae are harvested at the end of exponential and stationary phases. If cells are collected during exponential phase, sulfur cannot be completely consumed and as a result H_2 production decreases [50]. According to Kosourov et al. (2005), a periodic addition of sulfate causes a restoration of hydrogen generation [86]. Culture density also affects anaerobiosis in sulfur deprivation. A high cell density reduces light penetration which results in slowing photoinhibition and delaying anaerobic conditions [50]. Further studies need to be carried out in order to comprehend sulfur deprivation process and hydrogen production improvement. However, Barrows et al. (2008) simulated an experiment for *Synechocystis* sp. PCC 6803 to optimize the concentration of sulfur, nitrogen and carbon (the most essential nutrients for H_2 production). They found a maximum H_2 production rate of 0.81 ± 0.36 μmol H_2 mg Chl^{-1} h^{-1} under optimal concentrations of 20.1 μM sulfate, 0.52 μM ammonium, and 46 μM bicarbonate and they also reported the superiority of optimized sulfur and nitrogen to their deprivation [48].

3.4. Phosphorus

Phosphorus which is also essential for algal growth and H_2 production is provided for microorganisms in the form of organic or inorganic nutrients [75]. As about 1% of algal dry wt consists of phosphorus, any surplus of phosphorus leads to a decrease in the H_2 yield, whereas a deficiency of phosphorus impacts the photosynthesis activities as well as the biomass productivity; hence, an optimal concentration of phosphorous is required [77,87,88].

3.5. Microelements

Supplementation of organic and inorganic micronutrients (metal ions) is not only necessary for algal and cyanobacterial growth but also to activate enzymes to produce hydrogen [89,90]. The main and major microelements include sulfur, iron, magnesium, potassium, sodium, manganese, zinc,

cobalt, molybdenum, etc. that are presented in Table 4 [49]; each of these microelements has a specific function, and a deficiency in one of them will lead to a decrease in algal growth as well as H_2 production [85,89]. Iron is essential for H_2 production for those organisms relying on hydrogenase enzymes, which have a Fe–Fe center. A deficiency of iron induces a decline in cell density and size and inhibits protein synthesis [90]. It was found that high iron concentration led to a positive effect on cells due to the dependency of hydrogenase to iron [89]. Another study also demonstrated the importance of Fe for hydrogen production by cyanobacterium *A. halophytica* using different Fe^{3+} concentrations and it was concluded that the highest rate of H_2 production was obtained with 0.4 μM Fe^{3+} which resulted in 20 times more hydrogen than in an iron-free BG11 medium [79]. Magnesium and copper are vital and necessary for nitrogenase activity and algal photosynthetic mechanism. A molybdenum deficiency may affect nitrogen absorption at a cellular level [89].

4. Light requirements

Light is an essential component for algal and cyanobacterial growth as well as biohydrogen production, and it is supplied either naturally using sunlight or artificially by fluorescent lamps installed outside and inside of photobioreactors, depending on the species requirements [89]. As cell growth and H_2 production depend on light through photosynthesis to consume carbon to produce starch or glycogen for hydrogen production, a selection of an adequate light supply is a key factor to optimize not only phase 1 (photosynthesis) but also phase 2 (anaerobic phase for hydrogen production). Also, the degree of illumination will determine whether microorganisms are in the respiration phase (no light available), suffer from deprivation, are in the saturation phase, or experience photoinhibition [89]. Hence, the quantity, pattern, wavelength of light as well as photobioreactor configuration play an important role in the growth of microalgae and cyanobacteria.

i. Effect of wavelength on H_2 production

The photosynthesis process uses light energy in the range of 300–700 nm. It was reported that the most appropriate range of wavelength for bioH_2 production is 20–30 nm [50]. To achieve this wavelength, the selection of a light source is important. Light emitting diodes (LEDs) provide a narrow range of wavelength (20–30 nm) which leads to more hydrogen production compared to other sources of light such as monochromatic lights. Moreover, the spectral distribution of LEDs influences the rate of bioH_2 production [50,91]. Generally, white LEDs result in less bioH_2 than red and blue [91]. Salleh et al. (2016) investigated the effects of different color lights on hydrogen production by *A. variabilis* ATCC 29413 and they found that with an increase in the light intensity from 70 μE m^{-2} s^{-1} to 350 μE m^{-2} s^{-1}, the total hydrogen production using blue light was twice that obtained using white light. The H_2 production under blue light was due to an enhancement of light energy absorption in the blue spectrum (430–445 nm) and the nitrogenase enzyme was found to be more active in that range.

ii. Effect of the light pattern on H_2 production

The light pattern is another factor that has an effect on hydrogen production. Uyar et al. (2007) observed that hydrogen was produced throughout a light period while during a dark period, bioH_2 production was stopped [92]. However, other researchers claimed that cyanobacteria like *Anabaena* can produce hydrogen during the light period but also during the dark period due to their bidirectional hydrogenase enzyme [93]. Tamagnini et al. (2002) also believed that cyanobacteria benefit from dark periods because hydrogenase enzymes are really sensitive to O_2 produced under light periods, and having a discontinuous light (a light-dark cycle) will allow cyanobacterial strains to consume oxygen when they are in the dark and as a result avoid the inactivation of hydrogenases and bidirectional hydrogenase [94]. Marques et al. (2011) studied H_2 production by *Anabaena* sp. PCC 7120 (wild type and mutants) under an argon atmosphere at 54 μE m^{-2} s^{-1} light intensity and using a 16 h light/8 h dark cycle. It was reported that the amount of bioH_2 production by the wild strain under the 16:8 h cycle was the same as under continuous illumination, but the $hupL^-$, the $hoxH^-$ and $hupL^-$/$hoxH^-$ mutant strains produced 2.1, 1.5, and 1.9 times more hydrogen [59]. A study reported that the maximum hydrogen production by *C. vulgaris* was 530 ± 5 mL L^{-1} when cells were illuminated for 24 h followed by 24 h of darkness. When cells were exposed to continuous light for 3 days, H_2 production declined to 496 ± 4 mL L^{-1}. Seventy-two hours of darkness resulted in 348 ± 6 mL L^{-1}, while 1 day in darkness followed by 48 h of light resulted in 448 ± 4 mL L^{-1} [52]. These authors also studied H_2 production by *Microcystis aeruginosa* under darkness, light, and partial darkness (less than 24 h in darkness and then light applied). The maximum H_2 production was found to be 490 mL L^{-1} with light, while the highest H_2 volumes produced under full and partial darkness were 383 and 217 ± 3 mL L^{-1}, respectively [53]. Another work investigated the impact of three light-dark cycles (12:12, 14:10, and 18:06 h) on bioH_2 production by *C. reinhardtii* CC124 and compared it with continuous illumination at 70 ± 2 μE m^{-2} s^{-1}. It was observed that applying light-dark cycles instead of continuous illumination led to a significant decrease in total bioH_2 production from 210.91 ± 14.29 mL L^{-1} in 27 days–124.55 ± 9.10, 97.27 ± 9.10, and 92.73 ± 7.28 mL L^{-1} (in 27 days) under the daily cycles of 18:06, 14:10 and 12:12 h, respectively [70]. Although some studies have been carried out with certain strains, it is not exhaustive, and more research should be done with other strains to determine if the light pattern should be determined on a case-by-case basis or if it can be generalized for all strains. Also, it is still not clear whether a certain light pattern is optimum for both cell growth and hydrogen production or whether a different light pattern could be beneficial for cell growth and H_2 production.

iii. Effect of light intensity on H_2 production

Depending on each algal and cyanobacterial strain, the impact of light intensity on cell growth and hydrogen production varies. According to Laurinavichene et al. (2004), sulfur-deprived *C. reinhardtii* produced the maximum level of H_2 (130 mL L^{-1}) at a light intensity in the range of

20–30 μE m^{-2} s^{-1} after 120–150 h, but with an increase in the light intensity to 80 μE m^{-2} s^{-1}, the H_2 production decreased to 40 mL L^{-1} [12]. When investigating *C. reinhardtii* strain CC124, it was found that the optimum H_2 production (210.91 ± 14.29 mL L^{-1}) occurred at 70 μE m^{-2} s^{-1}, and increasing the light intensity from 70 to 100 μE m^{-2} s^{-1} showed a decrease in hydrogen production [70]. However, Tsygankov et al. (2006) observed that *C. reinhardtii* used a low light intensity of 25 μE m^{-2} s^{-1} for its growth, whereas the anaerobic conditions necessary for hydrogen production required higher light intensity of 110–120 μE m^{-2} s^{-1} [60]. *A. variabilis* ATCC 29413 also showed a similar trend when light intensity increased from 70 to 350 μE m^{-2} s^{-1}, the rate of hydrogen production declined, and the maximum hydrogen yield was achieved at 70 μE m^{-2} s^{-1} [71]. However, the rate of bioH_2 production by *Anabaena* sp. PCC 7120 and its mutants (hupL$^-$ and hupL$^-$/hoxH$^-$) increased from 0.9 to 4.3, 8.2 to 20.1, and 3.9–9.4 μmol mg^{-1} (Chl) h^{-1}, respectively, when increasing light intensity from 54 to 152 μE m^{-2} s^{-1}. Yodsang et al. (2018) also studied the effect of changing light intensity of (50, 100, 150, and 250 μE m^{-2} s^{-1}) on H_2 production by *C. elenkinii, F. muscicola, S. bohneri, N. calcicola* and *T. distorta*. They reported that the rate of hydrogen production increased with all strains except *N. calcicola* when increasing the light intensity to 250 μE m^{-2} s^{-1}, it increased 9 fold for *T. distorta*, 14 fold for *F. muscicola*, 27 fold for *C. elenkinii*, and 47 fold for *S. bohneri*, but *N. calcicola* produced the most hydrogen at a light intensity just under 100 μE m^{-2} s^{-1} [33]. Other authors also found that although *A. siamensis* TISTR 8012 was able to produce a maximum of 31 μmol H_2 mg^{-1} (Chl) h^{-1} at a light intensity of 200 μE m^{-2} s^{-1} by increasing light intensity from 40 μE m^{-2} s^{-1}, other cyanobacteria like *Anabaena* sp. PCC 7120, *Nostoc punctiforme* ATCC 29133, *and Synechocystis* PCC 6803 could only produce H_2 at a light intensity of 40 μE m^{-2} s^{-1} which was the same as the light intensity during the growth condition [64]. Zhang et al. (2015) investigated different light intensities for *cyanobacterium Cyanothece* sp. ATCC 51142 and found the highest hydrogen production at 247 μE m^{-2} s^{-1}, while 261 μE m^{-2} s^{-1} was the best light intensity for its growth condition [65]. Other researchers also reported that some cyanobacterial species need different light intensities for their growth (stage 1) and bioH_2 production (stage 2) [34]. However, other works stated that some cyanobacteria produced hydrogen under the same light intensity as their growth condition [68,72,83,95].

iv. Correlation of sulfur-deprivation and light intensity on H_2 production by microalgae

Rashid et al. (2013b) claimed that the rate of H_2 production is impacted by sulfur deprivation in the culture which strongly depends on the degree of light intensities used [50]. These authors applied four light intensities of (13, 34, 80, and 156 μE m^{-2} s^{-1}) for sulfur-deprived *C. reinhardtii* and found that increasing the light intensity accelerated the rate of sulfur deprivation [60]. Kim et al. (2006) also observed that when the light intensity increased to 200 μE m^{-2} s^{-1} for the same microalgae, the rate of sulfur consumption also increased which led to maximum H_2 production of 225 mL L^{-1}. Studies have also reported the alternation cycles of bioH_2 production by sulfur-deprived cells under light, for instance, the achievement of up to three cycles of hydrogen production [50]. Rashid et al. (2009) also claimed that sulfur-deprived *Microcystis aeruginosa* was able to produce hydrogen under complete light and dark conditions, whereas the amount of H_2 production was different [96]. However, the cost of sulfur deprivation process is affected by duration of light supply. It is claimed that more hydrogen was obtained under complete dark condition through sulfur deprivation process [97], however, an integrated light and dark condition is economically viable.

v. Correlation of light intensity and oxygen production on H_2 production

In cyanobacteria, the nitrogenase enzyme responsible for bioH_2 production is sensitive to oxygen because O_2 inhibits nitrogenase to produce hydrogen. Filamentous cyanobacteria such as *Anabaena* and *Nostoc* due to their heterocystous cells are able to separate N_2 fixation from O_2 evolution, while some non-heterocystous filamentous and unicellular cyanobacteria separate photosynthesis from N_2 fixation by restricting nitrogenase activity under dark conditions [98]. As O_2 evolution highly depends on light intensity and it is an inhibitor factor for H_2 production, evaluation of O_2 concentration is essential. Tsygankov et al. (1998) studied the effect of changing light intensity on O_2 evolution by *A. azollae* under a mixture of 2% CO_2 and argon atmosphere. They found that at light intensity of 20 μE m^{-2} s^{-1} when dissolved O_2 was 22 μM, no hydrogen was produced. Although an increase in light intensity increased H_2 production as well as dissolved oxygen, light intensity above 70 μE m^{-2} s^{-1} resulted in decreasing H_2 production and increasing O_2 evolution. They also observed that at constant light intensity of 140 μE m^{-2} s^{-1}, when the gas flow rate increased from 0.5 to 1.0 L min^{-1} there was a decrease of 28% in dissolved oxygen because of increased dilution, whereas H_2 production rate increased from 0.03 to 0.085 mL L^{-1} h^{-1} [28]. Borodin et al. (2000) applied a 12:12 light-dark cycle at light intensity of 332 μE m^{-2} s^{-1} with continuous aeration to investigate the impact of a light-dark cycle on O_2 evolution and H_2 production by *A. variabilis* PK84. During dark period, the concentration of dissolved oxygen dropped quickly from 380 to 160 μM because of the cell respiration and O_2 consumption as well as no photosynthesis and O_2 evolution. Also, at the beginning of darkness a rapid decline in hydrogen production was observed. However, through the first 3–6 h of light period and in the presence of a high O_2 concentration, hydrogen production increased [99]. Another study demonstrated that simultaneous O_2 and H_2 production by *Cyanothece* sp. ATCC 51142 under continuous illumination is not only a function of light intensity but depends on wavelength. At the lower wavelength (630 nm) and constant light intensity of 220 μE m^{-2} s^{-1} the maximum rate of O_2 production was 1.72 times higher than at 680 nm which led to a lower hydrogen production. At a constant wavelength and light intensities below 50 μE m^{-2} s^{-1} the rate of oxygen production was extremely low, however, increasing the light intensity increased both O_2 and H_2 production. At a higher light intensity of 140 μE m^{-2} s^{-1} O_2 evolution continued to increase whereas the rate of H_2 production remained steady [98].

vi. Effect of photobioreactor thickness and configuration on the light requirement for H_2 production

Factors such as depth, PBR material transparency and cell density in PBRs can all impact light penetration to algal and cyanobacterial species. The construction material providing the highest light transparency is glass (95%), followed by polymethyl methyl acrylate and polycarbonate (92%), polyethylene (80–85%), polypropylene and polyvinyl chloride (80%) (Dasgupta et al., 2010). The configuration and geometry of photobioreactors play an important role to provide an appropriate light requirement for cell growth and hydrogen production [100]. In this regard, transparency and the ratio of surface to volume of PBRs are important [89]. Besides, the distance between light sources and PBRs (installation of light sources inside and/or outside of PBRs) affects the cell growth and bioH_2 production; therefore, LEDs and immersed optical fibers as well as suspended materials scattering light in the culture allow the microorganisms to have better and more convenient access to light sources [53]. It was observed that the addition of silica nanoparticles in a 110 L tubular photobioreactor led to an increase in H_2 production from 1870 mL to 3121.5 ± 178.9 mL, compared to when the PBR was illuminated only at the surface [101]. More research is required for the search of cheap and efficient light scattering techniques in PBR.

A work investigated the effect of PBR diameter on the H_2 production by *C. reinhardtii* Dangeard C137+. Two bioreactors with the same design but with different diameters of 60 and 95 mm were used. It was observed that when the light intensity increased from 20 to 40 $\mu E\ m^{-2}\ s^{-1}$ in the larger PBR, the rate of H_2 production increased, but in the PBR with a smaller diameter when cells were exposed to the same range of light intensity, the total hydrogen production decreased, which highlighted the importance of the average light intensity inside the bioreactor on H_2 production instead of light intensity on the PBR surface [12]. Ainas et al. (2017) studied the effect of light intensity on bioH_2 production by *Spirulina platensis* in three different bioreactors (cylindrical, conical, and conical with an excavated base). They found that by increasing light intensity from 0.8 to 3 klx (Kilolux), the volume of hydrogen evolution in the cylindrical and conical PBR fluctuated, but in the conical with an excavated base, it increased to the highest level of 158 mL. They claimed that the latter design provided the largest illuminated surface of 255 cm^2 which was 2.5 times more than in the cylindrical and conical PBRs, and therefore reduced the dark zones and shade in high-density cell culture [102]. According to Oncel et al. (2015), when 2 sides of a magnetically mixed Roux-type photobioreactor were illuminated with the light intensity of 200 $\mu E\ m^{-2}\ s^{-1}$, the total H_2 production reached 110 mL L^{-1} which was not only higher than one-sided illumination under 400 $\mu E\ m^{-2}\ s^{-1}$ but also 22% more than the standard condition with 70 × 2 $\mu E\ m^{-2}\ s^{-1}$ [103].

5. Temperature requirements

Temperature is another essential factor for algal and cyanobacterial growth. Based on their optimum temperature range for growth, microorganisms are divided into three categories: mesophilic (temperature between 25 and 37 °C), psychrophilic (temperature between 5 and 20 °C), and thermophile (temperature above 50 °C) [8]. The optimal temperature for cell growth and H_2 production depends on the organisms, but the optimum temperature for stage I (photosynthesis) and stage II (hydrogen production) can also be different for each species. Most cyanobacteria can produce H_2 in the range of 30–40 °C [78]. While the optimum temperature for the growth of *Nostoc* was 22 °C, the highest rate of hydrogen production was achieved at 32 °C [104], and the optimum H_2 production for another subspecies (*Nostoc muscorum* SPU004) was found to be 40 °C [105]. In contrast, optimum hydrogen production from *A. variabilis* SPU 003 was observed at 30 °C [78]. Zhang et al. (2015) also investigated the effect of temperature on *Cyanothece* sp. ATCC 51142 cell yield (at 25, 30, 32, 35, 37, and 40 °C) and H_2 production (at 20, 25, 30, 35, 40, 47, and 55 °C). It was observed that the optimal temperature for biomass production was 37 °C which was higher than that for H_2 production (34 °C) [65]. Some researchers found that with an increase in temperature from 37 to 42 °C the maximum rate of H_2 production from *Microcystis aeruginosa* increased from 34 to 48 mL $L^{-1}\ h^{-1}$ [53]. *A. halophytica* also showed the same trend with increasing temperature from 25 to 35 °C [79]. According to Yodsang et al. (2018), the highest H_2 production by *C. elenkinii, F. muscicola, S. bohneri, N. calcicola* and *T. distorta* was obtained at 25 °C which was 1.2–1.6 times greater than at 30 °C [33]. However, in another study, higher hydrogen production from *Calothrix* 336/3 was found at 30 °C [106]. The increase in temperature from 37 to 40 °C also had a positive effect on the rate of hydrogen production from *Chlorella* sp. which increased from 183 to 238 mL $L^{-1}\ h^{-1}$ [107]. It was reported that 27 °C was the optimum temperature for H_2 production by *C. reinhardtii*, but it could also produce H_2 outdoors at 10 °C [103].

6. Effect of algal growth rate on H_2 production

Cyanobacterial and algal growth rate (biomass concentration) and culture age are other factors that can influence hydrogen production. To achieve an efficient hydrogen production, a high culture density of microalgae or cyanobacteria is necessary [108]. Vargas et al. (2018) studied the biomass yield of *Anabaena* sp. (UTEX 1448) under control and optimal conditions to compare biomass productivity and its effect on H_2 production. They observed that the highest biomass yield and growth rate of 675 ± 60 $g\ m^{-3}$ and 1.26 ± 0.04 d^{-1}, respectively were achieved under an optimum conditions of 32 °C, pH 10.2, 2.1 kg m^{-3} of glucose, 2220 lux, and nitrogen deprivation (10 g m^{-3} sodium nitrate). Then, the biomass harvested from the exponential phase was used for H_2 production. The results demonstrated that hydrogen production under optimal condition was 1.6 times greater than the control condition due to 38% increase in growth rate compared to the control conditions (24 °C, pH 9.2, 1.05 kg m^{-3} of glucose, 4440 lux) [29]. The same authors carried out another experiment by *Anabaena* sp. (UTEX 1448) to find the effect of cyanobacterial culture age on hydrogen production. Biomass collected from exponential and stationary phases was transferred to the second step for

hydrogen production which resulted in a higher hydrogen production rate in the exponential phase. They found that a younger culture in the exponential phase, despite having less biomass, were more metabolically active and could produce 4.1 times more H_2 than an older culture in stationary phase. Also, a higher biomass concentration limited light penetration in the PBR which led to a decrease in photosynthesis and an increase in respiration resulting a lower H_2 production in the stationary phase [109]. Although a dense culture is essential for hydrogen production, culture age must be taken into consideration. Another study also confirmed that the dependency of hydrogen production on the growth rate and culture age. H_2 production from Sulfur-deprived *C. reinhardtii* showed a linear relationship with cell concentration; when algal cell concentration increased from 5 to 20 μg Chl mL^{-1}, there was a moderate increase in H_2 production from 0.02 to 0.23 mL per mL culture. However, above 20 μg Chl mL^{-1} algal cell concentration, hydrogen production started to decrease. One reason that explained a decline in H_2 production was the production of by-products such as ethanol and organic acids in the stationary phase due to a higher cell density and older culture. Also, shading effects caused by the higher biomass concentration limited light penetration in the PBR that reduced H_2 production [110].

7. Mixed cultures for H_2 production

Hydrogen generation in microalgae is not continuous as the water-splitting activity of PSII and the hydrogenase systems are highly sensitive to oxygen [85]. Many studies showed that the hydrogen yield by co-culturing algae and bacteria was higher than in pure algal culture because bacteria can consume oxygen which otherwise is inhibitory for H_2 production by microalgae. Some bacteria may also consume carbohydrates stored by microalgae to generate H_2 under dark fermentation. A work demonstrated that co-culturing three strains of *C. reinhardtii* hemHc-lbac, cc124, and cc503 with *Bradyrhizobium japonicum* led to a 3.5-fold, 17-fold and 4.4-fold increase in hydrogen production, respectively [111]. An improvement in H_2 production by co-cultivating *C. reinhardtii* with *Azotobacter chroococcum* was also reported [112]. Another work also reported that when *C. reinhardtii* 704 was co-cultivated with *Escherichia coli*, *Pseudomonas stutzeri*, and *Pseudomonas putida*, H_2 production increased by 24%, 46%, and 32%, respectively [113]. Yu et al. (2021) also studied a co-culture of *C. reinhardtii* with *Mesorhizobium sangaii* which demonstrated a maximum H_2 production of 226.98 μmol mg^{-1} (Chl) using 3 g L^{-1} $NaNO_2$ and it was 5.2 times higher than the pure culture [114]. When *Chlorella* sp. MACC-360 was co-cultivated with *Bacillus amyloliquefaciens* and 8 g L^{-1} starch was used as a carbon source, the hydrogen production was three times higher than that with the pure algae [115]. However, the rate of H_2 production not only depends on algal strains due to their different carbohydrate accumulation but also depends on the choice of bacteria. Pandey et al. (2021) also studied hydrogen production by mixed culture of *Spirulina platensis* and *Bacillus firmus* NMBL-03, and they observed that at pH 6.5 and temperature of 32 ± 2 °C, the yield of H_2 was 1.92 ± 0.20 mmol (g COD reduced)$^{-1}$ [116]. *Scenedesmus Obliquus* was co-cultured with two bacteria *Enterobacter aerogenes* ATCC 13048 and *Clostridium butyricum* DSM 10702, which resulted in different H_2 production rates of 57.6 mL g^{-1} VS from 2.5 g L^{-1} wet biomass and 113.1 mL g^{-1} VS from 50 g L^{-1} dry biomass, respectively [117]. Other research investigated H_2 production from mixed culture when microalgae were cultivated in wastewater. It was reported that *S. Obliquus* and *Consortium C* were cultivated in urban wastewater in a 150 L-vertical tubular PBR and then they were used as a substrate for *Enterobacter aerogenes* in a dark fermentative process; the total H_2 production rates for both strains were found to be 2.96 and 2.91 mL, respectively, however, the specific hydrogen production rates were different (56.8 mL g^{-1} VS and 46.8 mL g^{-1} VS) due to the difference between volatile solid of *S. Obliquus* and *Con. C* [118].

8. Bioreactor design

Compared to open systems, photobioreactors (PBRs) or closed systems are able to control temperature, operation conditions, light penetration, contamination, and other factors which results in better microalgal growth and H_2 production [119]. It was reported that in a specific closed system, the rate of algae growth can be tripled [120]. To design an appropriate PBR for hydrogen production, some factors such as light penetration, large surface-to-volume ratio, temperature control, type of transparent and durable material for the construction of PBRs, gas exchange, and agitation methods play an important role as well as the selection of algal species and methods for hydrogen production. Hydrogen loss is also another important factor that must be taken into account for designing and using PBRs. Hydrogen leakage is caused due to the diffusion of gas through PBR materials and connections, as well as through the separation and extraction of hydrogen from the headspace of the PBR [121,122]. Also, the rate of hydrogen diffusion can be influenced by the surface area of the reactor. A larger surface area increases the opportunities for hydrogen molecules to escape from the system; hence, to minimize hydrogen leakage, all materials should have good properties with a low hydrogen permeability [123]. Moreover, all joints should have adequate seals that are made of high quality materials to prevent diffusion. Also, efficient stirring or mixing of the culture within the photobioreactor can aid in maintaining a uniform hydrogen concentration throughout a system, minimizing concentration gradients and reducing the driving force for diffusion. Techniques for proper agitation, such as sparging or mechanical stirring, can enhance gas mixing and subsequently decrease hydrogen losses [122]. According to Burgess et al. (2006), hydrogen collection efficiency (η_{coll}) is affected by reactor materials (hydrogen permeability coefficient), geometry of the reactor including wall thickness, reactor diameter, length of joints, gas and liquid velocities, and gas and liquid volume ratio [121]. Various types of PBRs have been used for hydrogen production, however, only some of them have been successful for large-scale application [1,51,124]. The following sections describe the advantages and shortcomings of the most common PBR designs.

9. Tubular reactors

Tubular reactors have different configurations which are classified into 3 main groups for hydrogen production [6,120]: i) vertical tubular reactors (VTR) such as airlift and bubble column, ii) horizontal tubular, and iii) helical tubular reactor. Availability of light for microorganisms and fluid dynamics in tubular reactors are essential factors of bioreactors design for their effective utilization [125].

i. Vertical tubular reactors (VTR)

The airlift and bubble column photobioreactors are considered VTR and have a few differences in their configurations, but both of them perform similarly. Compared to a simple bubble column, the internal-loop airlift reactor (ALR) shown in Fig. 1a, consists of concentric vertical tubes, namely the riser and downcomer [126]. Agitation and CO_2 supply for algal and cyanobacterial growth and H_2 production are achieved with a sparger at the bottom of the reactor [51]. Airlift bioreactors compared to other bioreactors like bubble columns and stirred tanks, benefit from more uniform mixing, high mass transfer, and less shear stress which not only makes them very popular in biological processes but also they are better for CO_2 uptake [124,127]; for example, CO_2 sequestration by *Spirulina* sp. in an ALR showed a high CO_2 removal efficiency [128]. The other advantages of these bioreactors consist of low material cost for their construction, high transparency, large surface-to-volume ratio, high biomass production, and better control of contamination. Some works have reported the usage of these reactors with various capacities and modifications for H_2 production [51,129,130]. In a recent study, the effect of gas velocity on hydrogen production in a 16 L airlift photobioreactor was investigated. It was reported that maximum H_2 production of 371 mL L^{-1} was achieved by *Anabaena* sp. at the gas velocity, light intensity, and temperature of 0.524 cm s^{-1}, 140 μE m^{-2} s^{-1}, and 30 °C, respectively (Table 5). This velocity was found to be optimal due to providing sufficient gas supplies and less shear stress [131].

Rectangular airlift photobioreactors like other airlift reactors benefit from excellent mixing and high photosynthesis efficiency, however, due to being difficult to scale up and the complexity of their construction, they are not recommended [132]. On the other hand, bubble columns have height limitations because CO_2 provided in the bubbles becomes depleted and dissolved oxygen increases [119]. Huang et al. (2017) stated that the height of ALRs cannot exceed 4 m due to mechanical strength despite providing a high concentration of CO_2 in the riser [133]. The type of agitation also creates challenges due to diluting the H_2 stream in the reactor. Gas transfer at the top of the photobioreactors, temperature control, and gas holdup are also major disadvantages of ALRs [51]. Bubble bursting also is another major demerit of ALRs as it can lead to high shear stress for surrounding cells. Moreover, light penetration, capital cost, and cleaning are other issues of this reactor [134].

ii. Horizontal tubular reactors (HTR)

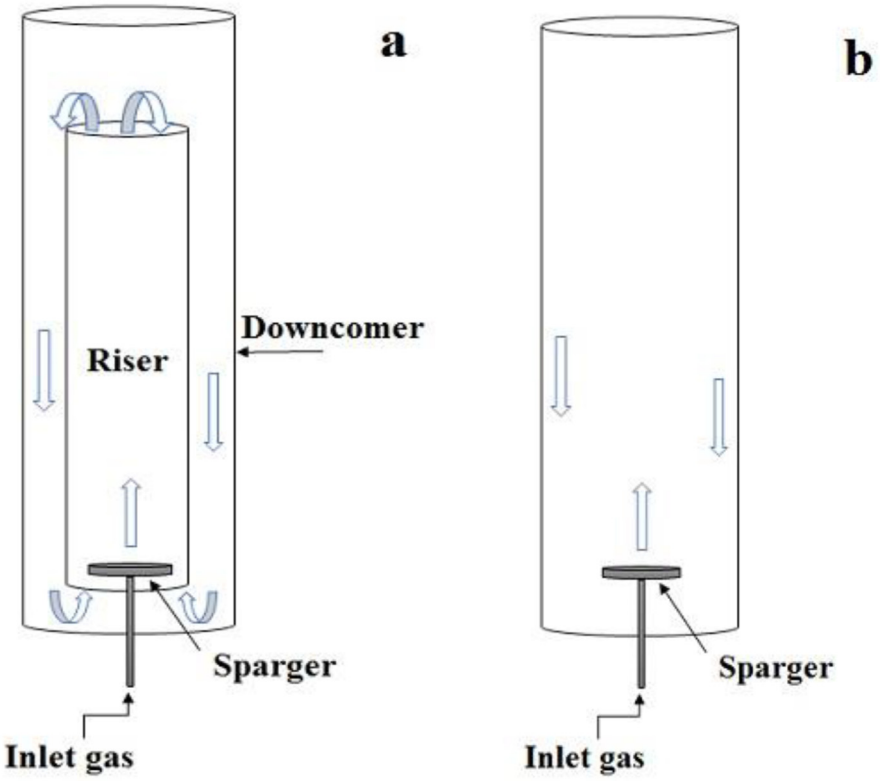

Fig. 1 – (a) airlift PBR, (b) Bubble column reactor.

Table 5 – Hydrogen production in tubular photobioreactors.

Photobioreactor type/ Configuration	Microorganism	Growth conditions	Hydrogen production conditions	H_2 production rate	Reference
Tubular PVC photobioreactor (2 L, 0.4 m high and 7.9 mm internal diameter)	*Anabaena variabilis* PK84	5% CO_2 and 95% air, 3 W m^{-2}	Using partial vacuum (250–300 torr) to reduce N_2	20 mL g^{-1} dry wt h^{-1} or 19 mL L^{-1} h^{-1}	[142]
Outdoor pilot scale horizontal tubular photobioreactor (50 L, made up of 10 parallel Pyrex glass tubes (length: 2 m, inner diameter: 4.85 cm), stainless steel basin (120 × 240 × 20 cm)	*Synechocystis* PCC 6803	medium BG11, sunlight, pH 7.4, 28.0 ± 0.5 °C, 97% air and 3% CO_2	nitrate-free growth medium ($BG11_0$), under N_2 atmosphere and dark environment, during 25 and 49 h	Total H_2 193.4 mL or 0.5 mL L^{-1} h^{-1}	[139]
Pilot scale tubular photobioreactor (110 L, Plexiglas tubes with 64 elements (inner diameter = 27.5 mm; outer diameter = 32 mm; L = 2 m)	*Chlamydomonas reinhardtii* CC124	TAP medium, 1000 + 1000 μE m^{-2} s^{-1}, 28 ± 5 °C, 97% air + 3% CO_2	sulfur-free TAP medium, 1000 + 1000 μE m^{-2} s^{-1} by scattering light silica nanoparticles in the PBR, after 24 h of sulfur deprivation without scattering light silica nanoparticles in the PBR	0.61 mL L^{-1} h^{-1} or 3121.5 ± 178.9 mL 0.42 mL L^{-1} h^{-1} or 1870 mL	[101]
Tubular photobioreactor (50 L, 10 parallel Pyrex glass tubes (length 2 m, inner diameter 4.85 cm)	*Chlamydomonas reinhardtii* CC124	TAP medium, pH 7.2 ± 0.1, 28 ± 0.5 °C, 250 μE m^{-2} s^{-1}, 97% air + 3% CO_2	sulfur-free TAP-S medium, after about 40 h of sulfur deprivation, under artificial light After 75 h of sulfur deprivation, under solar light (1850 μE m^{-2} s^{-1}) and 100 μE m^{-2} s^{-1} at night	0.17 mL L^{-1} h^{-1} or 850 ± 85 mL 930 ± 100 mL	[137]
Internal-loop airlift photobioreactor (16 L)	*Anabaena* sp.	$BG11_0$ medium, 140 μE m^{-2} s^{-1}, 30 °C, pH 8, 12 h:12 h light/dark cycle, batch mode	same as growth condition	Total H_2 371 mL after 7 days	[131]
Bubble column (1.08 L) (0.04 m diameter and 0.86 m height of photobioreactor)	Algerian microalgal strain	TAP medium, 7800 Lux, pH 7, 25 °C	sulfur-free TAP-S medium	–	[143]
Helical tubular (5 L, inner diameter 2 cm, outer diameter 2.4 cm and length = 1150 cm)	*Chlamydomonas reinhardtii* CC124	TAP medium, cool white fluorescent light, 150 μE m^{-2} s^{-1}, 27 ± 0.5 °C, pH 7.7, 97% air + 3% CO_2	sulfur-free TAP-S medium,	1.05 ± 0.05 mL L^{-1} h^{-1}	[141]
Helical tubular (4.35 L, made of PVC tubes with a 10 mm inner diameter, surface-to-volume ratio 200 m^{-1})	*Anabaena azollae*	Allen and Arnon medium, 30 °C, pH 7, 110–210 μE m^{-2} s^{-1}, 98% air + 2% CO_2	Allen and Arnon medium, batch mode,	13 mL L^{-1} h^{-1}	[28]
Indoor Helical photobioreactor (1.9 L, made of PVC tubes with 10-mm inner diameter)	*Anabaena* PCC 7120 *Anabaena* AMC 414	$BG11_0$ medium, 30 μE m^{-2} s^{-1}, 26 °C, bubbling with air same condition	Under Argon atmosphere, $BG11_0$ medium, 456 μE m^{-2} s^{-1} same condition	Maximum H_2 1.4 ± 0.3 mL h^{-1} L^{-1} $_{PBR}$ Maximum H_2 13.8 ± 1.5 mL h^{-1} L^{-1} $_{PBR}$	[144]
Outdoor Helical photobioreactor (4.35 L)	*Anabaena* AMC 414	$BG11_0$ medium, sunlight	Under Argon atmosphere, $BG11_0$ medium, Batch culture, after 150 h, maximum 30 °C and average 21.8 °C	Maximum H_2 14.9 mL h^{-1} L^{-1} $_{PBR}$	[144]
Automated Helical tubular photobioreactor (4.35 L)	*Anabaena variabilis* PK84	Air + 2% CO_2, 12-h light (36 °C) and 12-h dark (14–30 °C), 332 μE m^{-2} s^{-1}, during 2.5 months	same as growth condition	230 mL (12-h light)$^{-1}$ or 19.2 mL h^{-1}	[98]

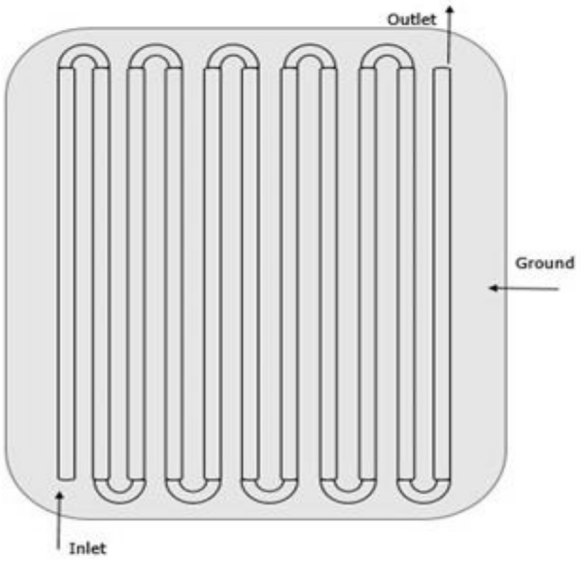

Fig. 2 – Horizontal tubular reactor.

Fig. 3 – Helical tubular reactor.

Horizontal tubular reactors Fig. 2 can be designed differently such as loop shape, α shape, set of parallel tubes, inclined manner, and near horizontal tubular bioreactors (NHTR). Given the flexibility of their design, they have been used in outdoor settings where high sunlight absorption and light conversion efficiency were reported [51,135,136]. In these types of reactors, gas is directly injected in either the tube connections or in the gas exchange unit, and agitation of culture in HTRs is achieved by mechanical pumps. Another advantage is the high surface-to-volume ratio. However, drawbacks include high energy consumption, biomass accumulation in the tubes, low gas exchange, low photosynthetic efficiency due to oxygen buildup which causes photobleaching and the major one is temperature control [6,51,122]. To solve the temperature problem, bioreactors are placed in temperature-regulated greenhouses in a cold climate, and a warm climate, bioreactors are cooled down by spraying water on the tube surface, shading tubes, submerging tubes into a pool of temperature-regulated water, or overlapping tubes [122,130]. A study used a 50 L horizontal photobioreactor inoculated with *C. reinhardtii* to compare H_2 production under artificial light (light intensity of 250 μE m^{-2} s^{-1}) with solar light (setting PBR outdoor). The results demonstrated a total hydrogen volume of 930 ± 100 mL under solar light that was 8.6% more than under artificial light [137] (Table 5). Another work investigated the hydrogen production by scattering light silica nanoparticles in a pilot scale HTR of 110 L and light intensity of 1000 + 1000 μE m^{-2} s^{-1} and found a maximum H_2 of 3121.5 ± 178.9 mL [101]. Vargas et al. (2014) also stimulated H_2 production in a pilot scale HTR with a working volume of 10,000 L by *Scenedesmus* sp. for 17 days, and it was observed that during aerobic conditions (10 days) the rate of H_2 was approximately zero, but after applying anaerobic atmosphere hydrogen was produced [138]. H_2 production from *Synechocystis* PCC 6803 in a 50-liter HTR was compared with the volume of hydrogen produced in a 0.5-liter glass bottle under the same operating conditions. It was reported that the amount of H_2 produced in the bottle was about 2.5 times higher than in the tubular photobioreactor [139].

iii. Helical tubular reactors

Helical tubular reactors (Fig. 3), also known as tubular coiled reactors due to their coiling configuration, are usually made of flexible plastics. To control the temperature, water is either sprayed, or cooling or heating coils are used. The agitation of culture is obtained by a centrifugal pump [51,130]. Although the high surface-to-volume ratio is one of the advantages of helical tubular reactors, they suffer from high energy input, low gas exchange, the accumulation of biomass in tubes, and high shear stress as a result, they have not been used widely for hydrogen production [122,140]. However, Oncel et al. (2014) studied H_2 production by *C. reinhardtii* in a tubular coiled photobioreactor and compared the rate of hydrogen produced in a flat photobioreactor under the same conditions (the light intensity of 150 μE m^{-2} s^{-1} and temperature of 27 ± 0.5 °C). They observed that due to less gas removed in the tubular coiled reactor, the rate of bioH_2 produced was 0.25 mL L^{-1} h^{-1} lower than in the flat reactor [141] (Table 5). Another study also investigated the hydrogen production by *A. variabilis* PK84 in an indoor helical photobioreactor at 332 μE m^{-2} s^{-1} and bioH_2 production was found to be 19.2 mL h^{-1} [98] (Table 5). Examples of hydrogen production in tubular PBRs are summarized in Table 5.

10. Flat plate reactors

Flat plate reactors are classified into 6 groups: vertical, curved-chamber, tilted flat panel (rocking motion), v-shaped, with baffles, and flat panel airlift (Fig. 4) which are all characterized by a high surface-to-volume ratio [145] and minimal thickness of the reactor [1]. Their advantages include a short light path which leads to even light distribution across the photobioreactor, low shear stress, low-cost materials, simplicity of construction, high mixing, and easy scale-up. Also, flat panel reactors have gained attention due to an open gas area which reduces the need to have a degassing unit [51,122]. In flat plate reactors, several techniques can be used for agitation like magnetic stirring, impeller stirring, baffles, rocking motion, or sparging which is the most common method. However, sparging results in the dilution of hydrogen gas and also recirculate gas produced in the system which may increase the risk of leakage [1,122,124]. Magnetic or impeller mixing requires high energy input. Rocking motion provides poor

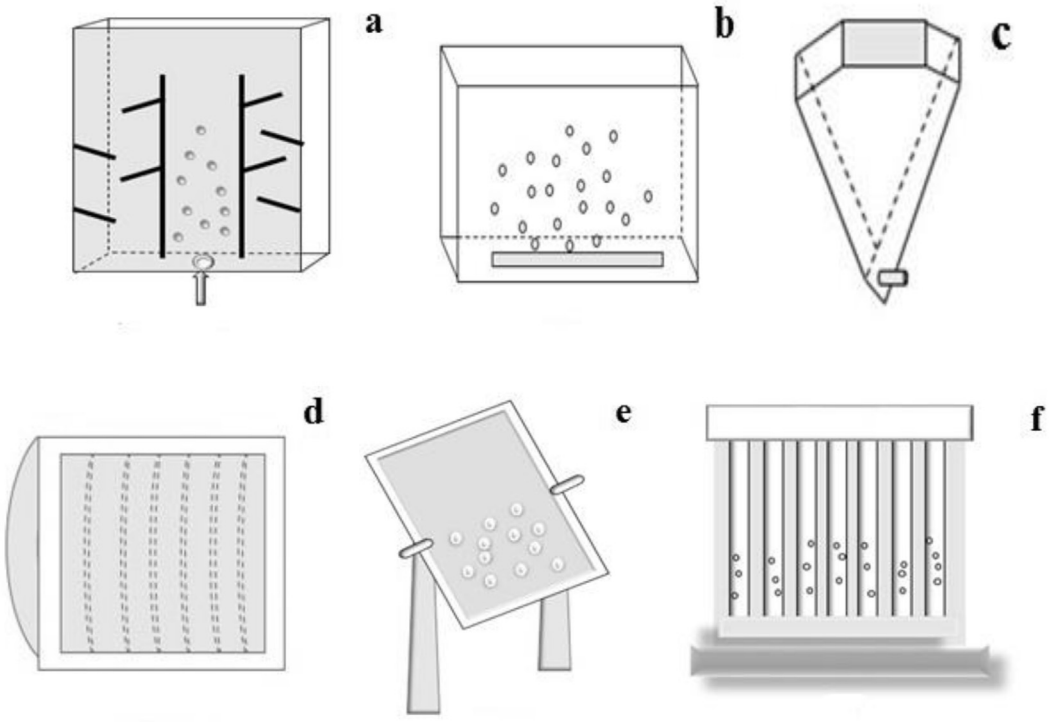

Fig. 4 – Flat reactors (a) flat plate with baffles, (b) flat plate airlift, (c) v-shaped. (d) curved-chamber, (e) tilted flat panel, (f) vertical.

agitation and is not usually used in H_2 bioreactors. A novel flat panel reactor designed by Skjånes et al. (2016) with a working volume of 1.62 L was investigated for H_2 production from sulfur-deprived *C. reinhardtii* at temperature and light intensity of 29 °C and 400 μE m^{-2} s^{-1}, respectively [122]. This reactor was used vertically for the cultivation of phototrophic species with air bubbling, but also horizontally when used for hydrogen production, in which mixing and gas exchange were carried out by a rocking motion. In the horizontal mode, the design created a large surface area between cells and head space which benefited H_2 release and collection. Tamburic et al. (2011) also designed a novel flat photobioreactor which consisted of two compartments. The first one was used for agitation of microalgae by recirculating gas, and the second one was applied to control temperature and wavelength. They studied hydrogen production by sulfur-deprived *C. reinhardtii* in this reactor and found that at the light intensity of 12 W m^{-2} (60 μE m^{-2} s^{-1}) and temperature of 25 °C, when algal cells were centrifuged, the highest H_2 production was 1.11 mL L^{-1} h^{-1} after 60 h [146]. However, when dosing sulfur and acetate, the hydrogen production reached 1.13 mL L^{-1} h^{-1} after 145 h at the optimal sulfur dosing rate of 0.042 mg SO_4^{-2} L^{-1} h^{-1}. Using optimized initial sulfate and acetate concentrations of 28 and 2550 mg L^{-1}, respectively, the H_2 production reached 1.52 mL L^{-1} h^{-1} after 170 h. It showed that H_2 production can be enhanced when the concentration of the nutrients is kept at the optimized initial levels [147] (Table 6). Nostoc PCC 7120 ΔhupW, a filamentous cyanobacterium, was also studied in a flat plate photobioreactor with a working volume of 3.85 L under aerobic and anaerobic conditions and light intensity of 44 μE m^{-2} s^{-1}. Under aerobic conditions, the highest H_2 production rate was found to be 1.9 mL h^{-1}, while under an argon atmosphere (anaerobic condition), it was 4.3 mL h^{-1}. However, when a mixture of 80% N_2 and 20% Ar was replaced with pure argon, the maximum hydrogen production rate reached 6.2 mL h^{-1} because under an Ar atmosphere, nitrogenase enzymes only produced hydrogen and there was no nitrogen-fixing activity [148] (Table 6). A number of studies carried out in flat PBRs are listed in Table 6.

11. Membrane photobioreactors

Membrane photobioreactors can have different configurations such as hollow-fiber, flat, and spiral sheets and the membrane is usually made of materials like cellulose acetate and nitrate, polyvinylidene difluoride, polysulfone, polypropylene, etc. [142]. Markov et al. (1993, 1995) designed a hollow-fiber photobioreactor (Fig. 5) composed of hydrophilic cuprammonium rayon hollow fibers and was used for continuous hydrogen production. Cells were immobilized on the outer surface of fibers and the dissolved H_2 diffused from the medium to the inner surface of fibers (lumen space) and then went through a gas column to be collected. The most important advantage of this configuration is the selective separation of cells and dissolved hydrogen [150,151]. However, membrane fouling occurs over time and periodic cleaning with chemicals or replacement is a major drawback. Markov et al. (1993) reported a maximum hydrogen production of 20–200 mL h^{-1} g^{-1} dry wt by immobilized *A. variabilis*

Table 6 – Hydrogen production in flat photobioreactors.

Photobioreactor type/Configuration	Microorganism	Growth conditions	Hydrogen production conditions	H_2 production rate	Reference
Lab scale Flat photobioreactor (1.1 L)	*Chlamydomonas reinhardtii* L159I –N230Y	TAP medium, 97% air + 3% CO_2, 70 μE m^{-2} s^{-1}, pH 7.2 ± 0.1, 28 ± 0.5 °C	sulfur-free TAP-S medium, after 75 h of sulfur deprivation	5.77 mL L^{-1} h^{-1}	[149]
Flat panel (5.5 L, total height 26.5 cm, width 35.5 cm, and depth of 5.9 cm)	*Chlamydomonas reinhardtii* CC124	TAP medium, cool white fluorescent light, 150 μE m^{-2} s^{-1}, 27 ± 0.5 °C, pH 7.7, 97% air + 3% CO_2	sulfur-free TAP-S medium	1.3 ± 0.05 mL L^{-1} h^{-1}	[141]
Lab scale horizontal Flat photobioreactor (1.6 L, the outer size 240 × 360 × 40 mm (width × Height × Depth), the inner size (180 × 300 × 30 mm)	*Chlamydomonas reinhardtii* NIVA CHL153	acetate-free TAP-ac medium, 29 °C, 400 μE m^{-2} s^{-1}, air + 2.5% CO_2	acetate-free TAP-ac medium, 29 °C, 400 μE m^{-2} s^{-1}	–	[122]
Novel Flat-plate photobioreactor (3.9 L, dual-compartment reactor body dimensions were 250 × 240 × 65 mm (height × width × thickness)	*Chlamydomonas reinhardtii*	TAP medium, constant cool-white LED irradiation of 8.6 W m^{-2}, 20 °C	sulfur-free TAP-S medium, 20 °C, during 60 h	H_2 yield of 105 mL $L^{-1}_{culture}$ or maximum H_2 1.11 mL L^{-1} h^{-1}	[146]
Flat-plate Photobioreactor (3.9 L)	*Chlamydomonas reinhardtii* cc124	TAP medium, 12 W m^{-2}, 60 μE m^{-2} s^{-1}, 25 °C	under controlled sulfur and acetate uptake with 28 mg L^{-1} initial sulfate and 2550 mg L^{-1} initial acetate Sulfur dosing, under anaerobic conditions	Maximum H_2 1.52 mL L^{-1} h^{-1} or H_2 yield of 119.8 mL L^{-1} Maximum H_2 1.13 ml L^{-1} h^{-1}	[147]
Flat panel Photobioreactor (3.85 L and, the size of the active surface (polycarbonate plates) 200 × 600 mm and culture depth 30 mm)	*Nostoc* PCC 7120 ΔhupW	Bubbling with air, $BG11_0$ medium, pH 8, 30 °C, 44 μE m^{-2} s^{-1}	same as growth conditions, during 74 h	Maximum H_2 1.9 mL L^{-1} h^{-1},	[148]
Flat panel Photobioreactor (3.85 L, polycarbonate plates 200 × 600 mm and culture depth 30 mm)	*Nostoc* PCC 7120 ΔhupW	Under Argon, $BG11_0$ medium, pH 8, 30 °C, bubbling with air, 44 μE m^{-2} s^{-1}	The same as growth condition, during 104 h	Maximum H_2 4.3 mL L^{-1} h^{-1},	[148]
Flat panel Photobioreactor (3.85 L, polycarbonate plates 200 × 600 mm and culture depth 30 mm)	*Nostoc* PCC 7120 ΔhupW	With 80% N_2 + 20% Ar, $BG11_0$ medium, pH 8, 30 °C, bubbling with air, 44 μE m^{-2} s^{-1}	Under Ar atmosphere, during 128 h	Maximum H_2 6.2 mL L^{-1} h^{-1},	[148]

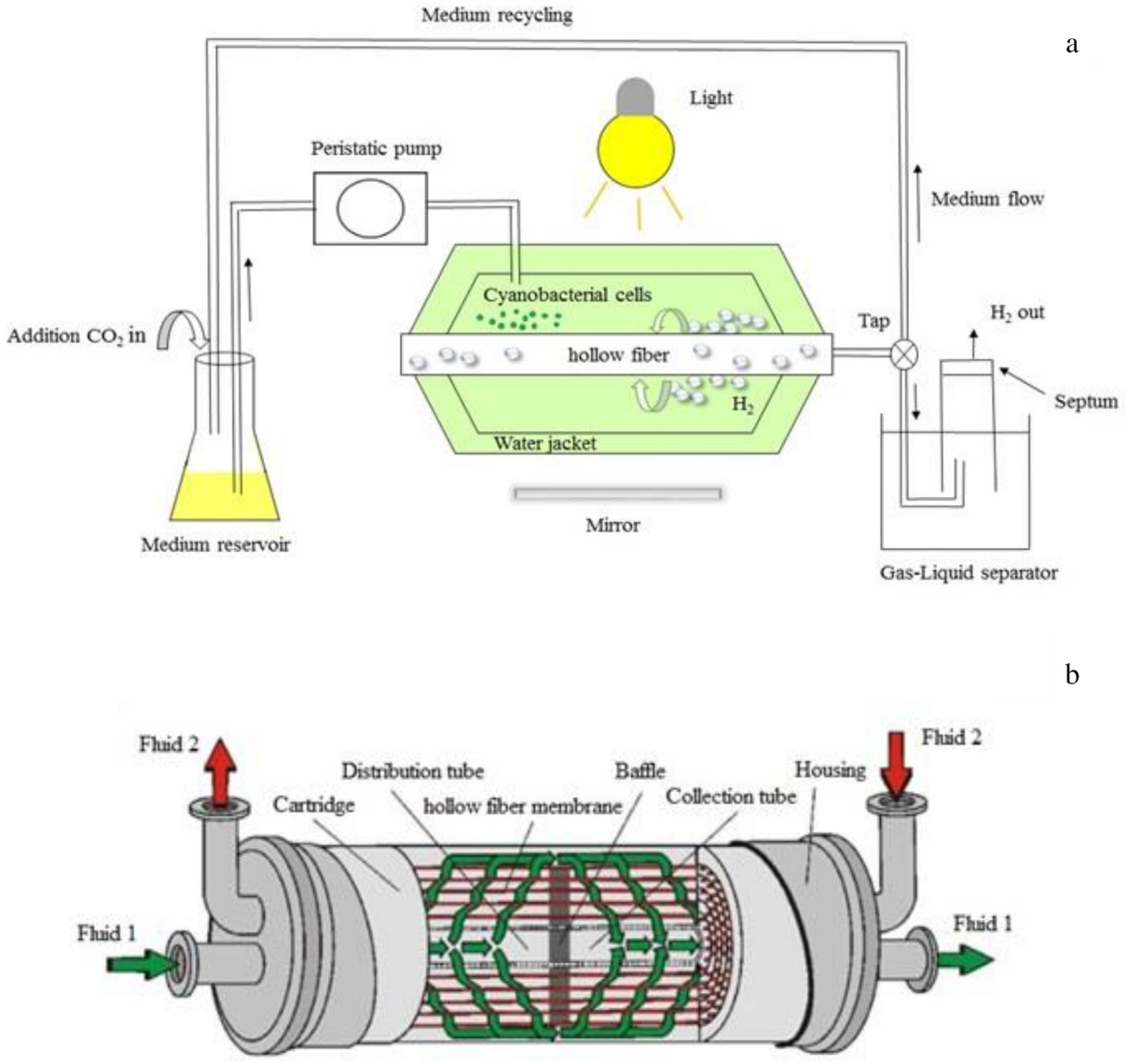

Fig. 5 – (a) schematic of H_2 production by cyanobacteria in a membrane photobioreactor; adapted from Ref. [150]. (b) hollow-fiber membrane; adapted from Ref. [153].

cultivated in Allen-Arnon medium over a 5-month period [150] (Table 7). This reactor was also applied for H_2 production and cleaning up water from ammonium ions simultaneously by the same strain when 0.5 mg L^{-1} ammonium ions were added to the Allen-Arnon medium (Table 7) [80]. The benefit of the application of this reactor was due to the diffusion of ammonium through membranes, while cells penetration did not happen because of their larger diameter, and it was observed that the maximum hydrogen production was 20 mL g^{-1} dry wt h^{-1} as well as 90% ammonium uptake efficiency. However, there is a lack of studies of membrane fouling in these reactors cultivating microalgae and cyanobacteria. The cultivation gases include H_2, O_2, N_2, and CO_2, but the laboratory scale studies have not attempted to concentrate or purify H_2 which remains an obstacle for large-scale applications.

12. Electrochemical sequential batch reactor (ESBR)

This type of reactor is made up of two compartments (Fig. 6) and works similarly to a microbial electrolysis cell (MEC); in both systems, protons (H^+) which are produced at the anode, are transferred to a second chamber through a cation exchange membrane (CEM) and due to a small voltage between the cathode and anode, H_2 is generated [154–156]. However, in ESBR, hydrogen can be produced in both the anodic and cathodic chambers; microalgae in the anode chamber produce biohydrogen, while electrochemical H_2 is formed in the cathode chamber by the addition of small voltage [157]. Hasnaoui et al. (2020) designed an ESBR, a novel PBR, with a double chamber consisting of 6.5 cm diameter and 16 cm height

Table 7 – Hydrogen production in membrane photobioreactors.

Photobioreactor type/ Configuration	Microorganism	Growth conditions	Hydrogen production conditions	H_2 production rate	Reference
Sixty hollow-fibers photobioreactor (Hydrophilic cuprammonium rayon, inner diameter 200 μm)	Immobilized *Anabaena variabilis* ATCC 29413	Allen-Arnon medium + 0.5 mg L^{-1} ammonium ions, Light intensity at the top surface 15 μE m^{-2} s^{-1}, Light intensity at the bottom surface 5 μE m^{-2} s^{-1}, 24–25 °C	Heating cell growth medium at 55 °C next flushing with Ar, during 3 months	The highest H_2 20 mL h^{-1} g^{-1} dry wt or 67 mL h^{-1} L^{-1}	[80]
laboratory-scale hollow-fiber bioreactor (the total surface area of hollow fibers was 0.8 m^2)	Immobilized *Chlamydomonas reinhardtii* CC-503 cw92 mt^+	CO_2 and air, 15 μE m^{-2} s^{-1}	partial vacuum, during six months	6.0 mL h^{-1} g^{-1} dry wt	[152]
Sixty laboratory-scale hollow-fibers bioreactor (Hydrophilic cuprammonium rayon, innerdiameter 200 μm, medium reservoir 750 mL, gas phase 400 mL)	Immobilized *Anabaena variabilis*	Allen-Arnon medium, 25 °C, Light intensity at the top surface 25 μE m^{-2} s^{-1}, Light intensity at the bottom surface 13 μE m^{-2} s^{-1}	Heating cell growth medium at 55 °C next using partial vacuum (270–300 torr) + injection of 320 mL CO_2, over 1 year	20 mL h^{-1} g^{-1} dry wt	[151]
laboratory-scale hollow-fiber bioreactor (type AM 100 L (Asahi), Length of the column 110 mm, volume 15 mL)	immobilized *Anabaena variabilis*	Allen-Arnon medium, 28 °C, 60 μE m^{-2} s^{-1}	Heating cell growth medium at 55 °C next using partial vacuum (500 torr), for 5 months	20–200 mL h^{-1} g^{-1} dry wt	[150]

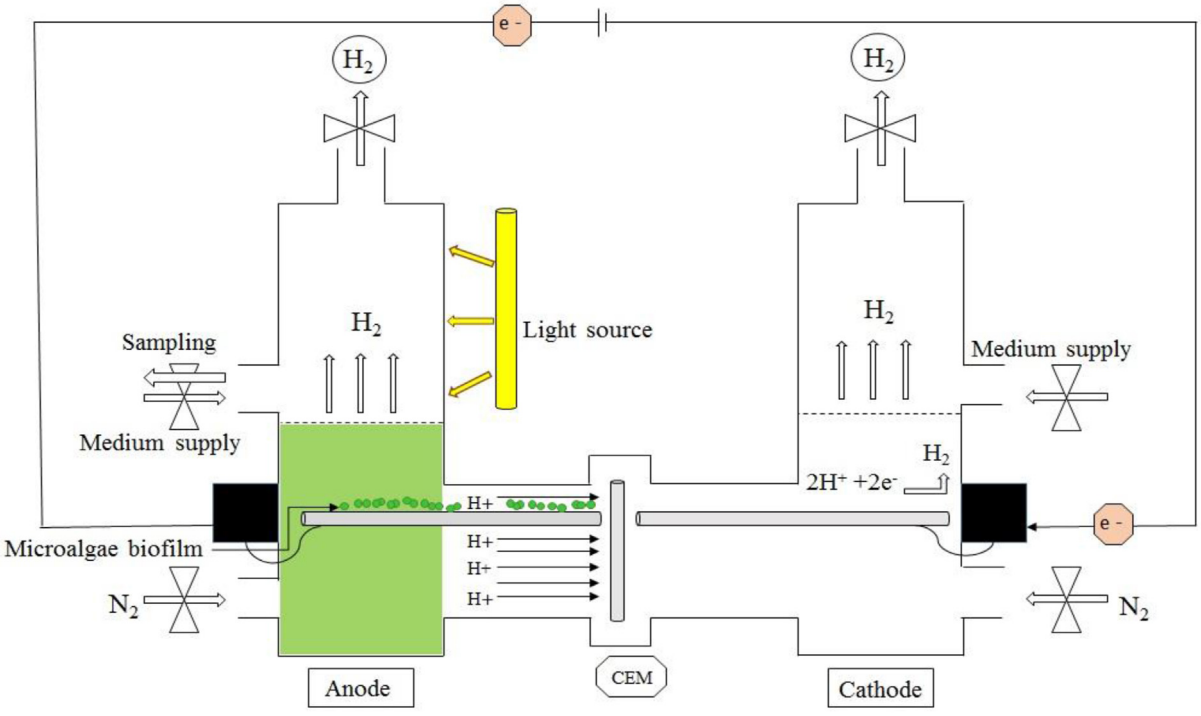

Fig. 6 – Electrochemical sequential batch reactor (ESBR) for H_2 production by cyanobacteria and microalgae; adapted from Ref. [157].

(including cylindrical Pt electrode with 8 cm length, 0.5 cm diameter, and 12.56 cm^2 surface area) to study hydrogen production from *Spirulina* sp. under the light intensity of 2.92 W m^{-2}, 12; 12 light-dark cycles, pH 9.5, temperature 35 °C, and Zarrouk medium. It was reported that H_2 generation at the cathode was 13.37 mol H_2 d^{-1} m^{-3}, whereas *Spirulina* was able to produce an additional 27.49 mol H_2 d^{-1} m^{-3} in the anodic compartment under the light intensity of 2.92 W m^{-2} [157]. This is a 50% increase when *Spirulina* is combined with a MEC which is not negligible. Further research should be carried out on these systems and how to optimize the H_2 from both, microbial and electrochemical routes.

13. Conclusions

Microalgae and cyanobacteria are good candidates for H_2 production and they can also be cultivated with bacteria to improve the rate of H_2 production. Amongst microalgae, it is worth mentioning *Tetraspora* who achieved 1.18 μmol H_2 mg^{-1}_{cell} h^{-1} and *C. reinhardtii* who achieved 8.8 mL H_2 L^{-1} h^{-1} after 49 h, but these yields were obtained in small laboratory tubes and may not be reproducible on large scale. As far as cyanobacteria are concerned, *Nostoc linckia* was reported to have produced 105 μmol H_2 mg^{-1}_{chl} h^{-1} while *A. variabilis* was found to have produced up to 46 mL L^{-1} h^{-1} and 7.73 mL $g^{-1}_{dry\ cell}$ h^{-1}. However, important factors must be carefully considered on a case-by-case basis such as optimal concentration and suitable carbon, nitrogen, presence of dinitrogen gas in headspace and phosphorus sources and microelements, optimum temperature, culture density and age (exponential vs stationary phase of cells) and illumination (light intensity, wavelength and light/dark cycles). More detailed studies of the light intensities required at each stage of sulfur deprivation is also recommended. Strategies such as anaerobic atmosphere, co-cultures, cell immobilization and sulfur deprivation have also been shown to be successful with specific strains. The gas flowrate and composition were also found to significantly affect hydrogen production in specific strains.

The selection of a type of PBR also influences hydrogen production. Tubular, flat, and hollow-fiber PBRs are the most promising reactors for hydrogen production, however, among PBRs flat panel have gained more attention due to the ease of their construction and having a high surface to volume ratio which resulting in a superior distribution of light. Among the most recent studies, it is worth mentioning *A. variabilis* who achieved 19 mL L^{-1} h^{-1} in a tubular PBR and 67 mL L^{-1} h^{-1} in a membrane PBR using immobilized cells. This is equivalent to 20 mL $g^{-1}_{dry\ cell}$ h^{-1}. In flat PBR, up to 6.2 mL L^{-1} h^{-1} was achieved by *Nostoc*, but none of the studies demonstrate economic viability of the process nor provided capital and running costs associated with each PBR. Recently, an electrochemical reactor was combined with microbial systems which demonstrated a significant improvement in H_2 production. The inclusion of nanoparticles is an interesting option to improve light scattering in a photobioreactor. However, it is necessary to investigate the cost of any PBRs for hydrogen production in both lab and large scales and compare them to select the most cost-effective system producing a high yield of H_2 per volume of reactor. Also, the hydrodynamic parameters of PBRs must be studied to find the optimal flow rates and mixing to avoid dead zones which have a significant effect on H_2 production. At a large scale, nutrient levels should be carefully monitored to maintain optimum conditions for continuous H_2 production.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ijhydene.2023.09.108.

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