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## Review

# Harnessing photosynthesis for materials, devices, and environmental technologies

Fan Jiang<sup>1</sup>, Friedrich H Kleiner<sup>1</sup> and Marie-Eve Aubin-Tam



Photosynthetic organisms convert solar light into chemical energy through the process of photosynthesis. The employment of photosynthetic organisms in novel materials and devices provides them with a solar-powered and sustainable functionality. In general, photosynthesis utilizes light, water, and CO<sub>2</sub> to generate various organic compounds while releasing secondary valuable products such as O<sub>2</sub>, extracellular electrons, carbohydrates, or H<sub>2</sub>. The light-dependent inputs and outputs are harnessed for environmental purification, biomedical applications, and production of biofuel, electricity, nanomaterials, or bioplastics. In this review, we summarize photosynthesis-assisted materials and engineering applications based on the products and substrates of photosynthetic processes, and we highlight key challenges that remain to be addressed.

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## Introduction

Photosynthetic organisms convert light into chemical energy through photosynthesis, serving as the primary producers at the foundation of many ecosystems and food chains. Oxygenic organisms (plants, algae, certain types of cyanobacteria) use water and CO<sub>2</sub> to produce carbohydrates with O<sub>2</sub> as a byproduct (Reaction 1) [1].



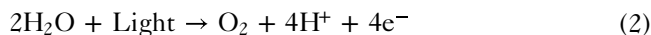
Complex biochemical processes are involved in carrying out these seemingly simple chemical reactions in photosynthesis. Reactants and end products of photosynthesis as well as underlying regulative mechanisms can be utilized in light-driven materials and devices, while endowing sustainable, biocompatible or regenerative features difficult to achieve in traditional systems.

This paper gives an overview of technologies that directly or indirectly utilize photosynthesis. First, the biological process of photosynthesis is presented with focus on the main reactants and end products. Then, applications associated with photosynthetic reactants (CO<sub>2</sub>), photosynthetic end products (O<sub>2</sub>, carbohydrate), or photosynthetic regulative mechanisms (electron export, H<sub>2</sub>) are presented.

## Reactants and end products of photosynthesis

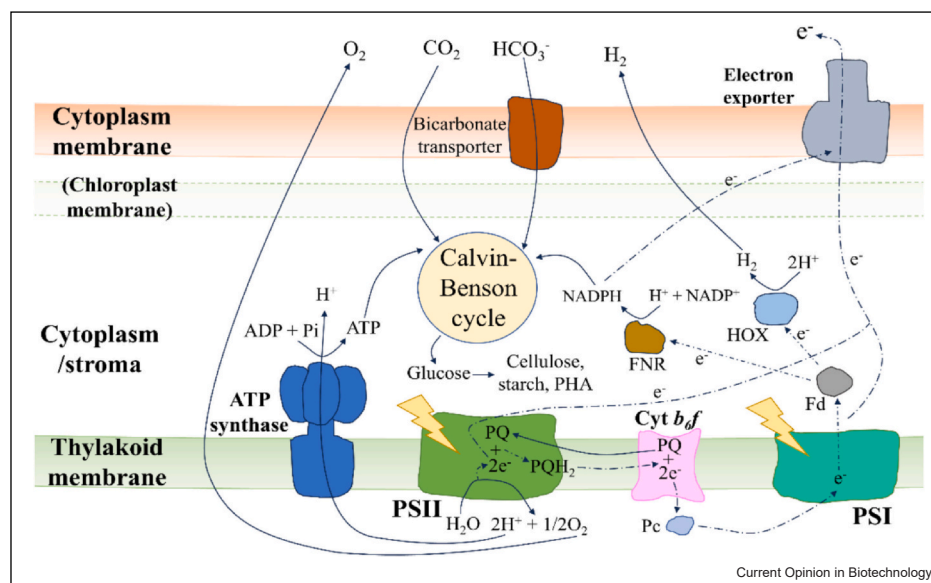
### Light reaction

Photosynthesis is divided into the light reaction and the dark reaction (Figure 1). The light reaction starts in a transmembrane protein complex located in thylakoid membranes of cyanobacteria and chloroplasts called photosystem II (PSII), where photons excite electrons in chlorophyll pigments. The energy is passed from pigment to pigment until it reaches the chlorophyll of the P680 reaction center. After P680 excitation, an electron is released into the photosynthetic electron transport chain, resulting in the formation of cationic P680<sup>+</sup>. The missing electron of P680<sup>+</sup> is replaced through the splitting of water at the O<sub>2</sub> evolving complex located in the luminal part of PSII. Each water molecule releases 2 electrons to regenerate P680 with ½ O<sub>2</sub> and 2H<sup>+</sup> as bi-products (Reaction 2). While some O<sub>2</sub> is used for respiration, the majority diffuses to the extracellular environment.



Plastoquinone (PQ), a hydrophobic electron carrier, collects two excited electrons at PSII and is converted to plastoquinol (PQH<sub>2</sub>). PQH<sub>2</sub> then diffuses through the thylakoid membrane to cytochrome *b<sub>6</sub>f* complex (Cyt *b<sub>6</sub>f*), where PQH<sub>2</sub> molecules are oxidized and transfer electrons to hydrophilic, luminal electron carriers plastocyanin (Pc) or cytochrome *c<sub>6</sub>* (Cyt *c<sub>6</sub>*). This process releases energy and fuels the dislocation of H<sup>+</sup> to the lumen at Cyt *b<sub>6</sub>f*, contributing to the H<sup>+</sup> gradient across the thylakoid membrane. Pc or Cyt *c<sub>6</sub>*

Figure 1



Schematic diagram of biological processes involved in light reaction, carbohydrate production, hydrogen production, and electron export in a photosynthetic cell. Dotted lines indicate electron transport pathways. Photosystem II (PSII), photosystem I (PSI), cytochrome *b<sub>6</sub>f* complex (Cyt *b<sub>6</sub>f*), hydrogenase complex (HOX), ferredoxin (Fd), ferredoxin-NADP<sup>+</sup> reductase (FNR), polyhydroxyalkanoate (PHA). Electron export is displayed vaguely since underlying electron carriers and transporters vary between lineages and/or are poorly understood.

transfers the electrons to photosystem I (PSI). PSI works in a similar manner to PSII, and the electrons excited here are transferred to ferredoxin (Fd) located at the stromal side of PSI. Fd donates electrons to ferredoxin-NADP<sup>+</sup> reductase (FNR), which in turn reduces NADP<sup>+</sup> to NADPH.

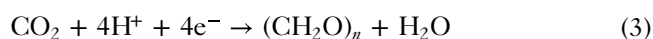
The H<sup>+</sup> gradient facilitated at the thylakoid drives a transmembrane protein complex called ATP synthase. Here, the H<sup>+</sup> in the lumen follow their electrochemical gradient and return through the ATP synthase to the stroma. This drives a spectacular molecular machinery that regenerates ATP.

### Dark reaction

In the dark (=light independent) reaction of photosynthesis, inorganic carbon is fixed into organic carbohydrates through the Calvin-Benson cycle (CBC; Reaction 3). This reaction takes place in the stroma of chloroplasts or cytosol of cyanobacteria.

In aquatic environments, the predominant type of dissolved inorganic carbon (DIC) depends on pH (acidic: H<sub>2</sub>CO<sub>3</sub>/CO<sub>2</sub>; neutral: HCO<sub>3</sub><sup>-</sup>; alkaline: CO<sub>3</sub><sup>2-</sup>). DIC either diffuse passively or are transported actively (carbon concentrating mechanism) to the CBC. Then, the enzyme ribulose-1,5-bisphosphate carboxylase-oxygenase fixes molecular CO<sub>2</sub> into the C5-sugar ribulose-1,5-bisphosphate, creating two C3-sugars of 3-phosphoglycerate. Subsequent steps of the CBC require NADPH and ATP from the

light reaction, eventually forming the C6-sugar glucose. Glucose can be further processed into polysaccharides for energy storage (starch) or building blocks (cellulose).



### Applications based on photosynthetically produced O<sub>2</sub>

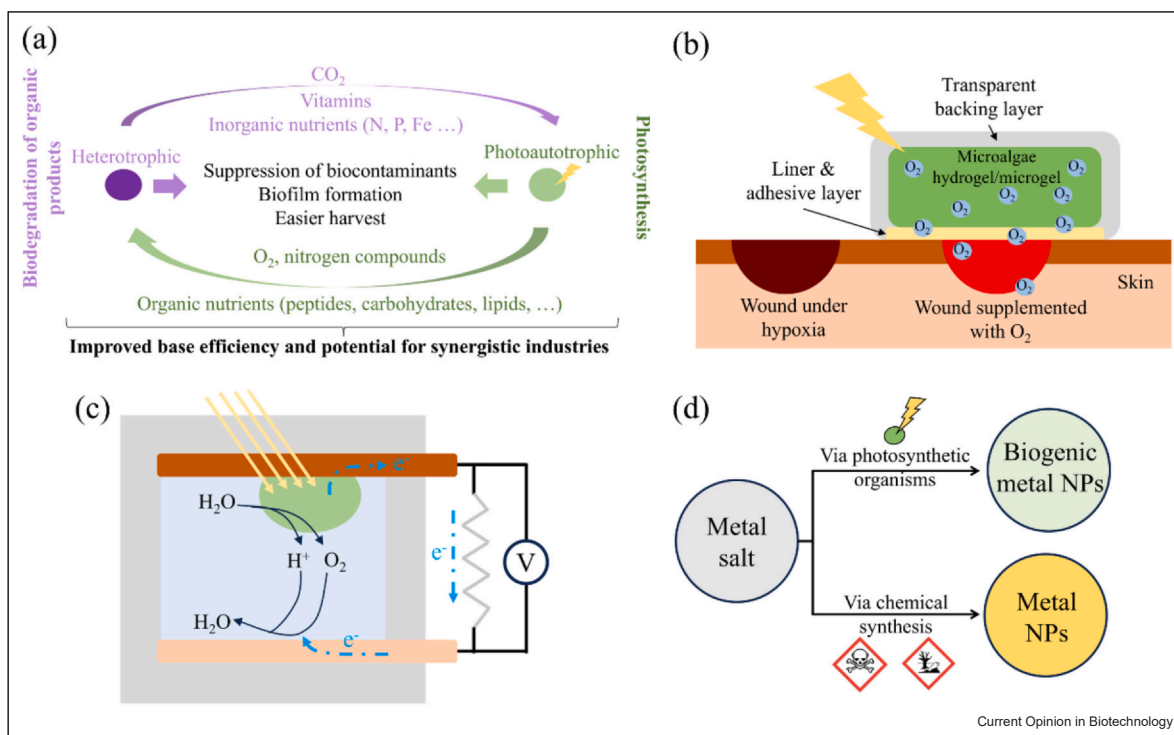
Any organism performing aerobic respiration uses O<sub>2</sub> as final electron acceptor, forming H<sub>2</sub>O. Various industrial and medical applications demonstrate the increased performance of respiring cells when O<sub>2</sub> is supplied by photosynthetic organisms (Figure 2a,b) [2,3].

### Photosynthetic organisms in synergistic industries

Co-culturing photosynthetic and respiratory organisms in symbiotic consortia is explored in industry for increased efficiency, robustness toward biocontamination (e.g. outgrowth), self-reliance (e.g. vitamin/nutrient exchange), or scalability of both heterotrophic and autotrophic partner alike (Figure 2a).

For example, O<sub>2</sub> supplied by photosynthetic organisms in municipal wastewater treatment reduces total energy requirement by 40–60% [4], as it eliminates the need for artificial aeration while still allowing biological oxidation of organic matter by aerobic microorganisms. Moreover, the presence of microalgae improves the assimilation of

Figure 2



Applications based on photosynthetically generated  $O_2$  and electrons. **(a)** Symbiotic relationship between heterotrophic and phototrophic processes for synergetic industries. **(b)** Microalgal hydrogel/microgel medical patch that releases oxygen to wound under hypoxia. **(c)** Design of biophotovoltaic systems used to harvest bioelectricity from an oxygenic biofilm attached to an anode. An anode receives electrons from photosynthetic organisms, and a catalytic cathode enables the terminal electron acceptor reaction (e.g.  $O_2 + 2H^+ \rightarrow H_2O$ ). **(d)** Chemical synthesis and photosynthesis for producing metal nanoparticles (NPs) from metal salts.

excess nitrogen or phosphate species up to 90% [5]. Similarly, including microalgae in aerobic microbial fuel cells eliminates the need for artificial aeration to supply  $O_2$  as the final electron acceptor at the cathode. Additionally, algae provide nutrients or  $O_2$  to electrochemically active microorganisms at the anode.

Further promising examples in which microalgae assist bacteria through  $O_2$  supply include bioremediation [6], production of biofuels [7], or biogas purification [2]. Likewise, bacteria can also assist algae, for which some examples will be presented in the following sections. However, a common limitation is the challenge of matching growth rates of symbiotic partners under changing environmental conditions (e.g. light access), which can introduce competition or toxicity effects (e.g. pH,  $NH_3$ , etc.) if unbalanced.

### Photosynthetic organisms in medical applications

Both chronic wounds and cancer tissues are characterized by hypoxia due to damage or outgrowth of vascular systems, respectively. Localized supplementation of  $O_2$  is occasionally employed for wound and cancer treatments, but techniques vary greatly in dose control,

continuity in  $O_2$  supply, convenience, side effects, or costs. These include high-pressure chambers, electric  $O_2$  generators, or chemicals [8]. Among these, a relatively convenient approach is described as chemical oxygen production therapy, which provides  $O_2$  through administration of nanoparticles (NPs) or  $H_2O_2$ -decomposing nanocarriers [9] but poses challenges related to low control of lifetime, dosage, or spatial distribution.

Microalgae are explored as an alternative to improve local  $O_2$  supply in wounds [10–12] (Figure 2b) and cancer tissues [3,13,14]. They are typically incorporated into hydrogels or microspheres [15] to improve administration, lifetime, and diffusion of dissolved  $O_2$ . Some gel polymers such as pluronic F-127 can be printed, enabling control over 3D shape and direct deposition into wound beds [16]. Low surface attachment of gels is a reoccurring problem but was improved by including adhesives such as chitosan [17] or polydopamine [16]. Co-culture of biocompatible bacteria and microalgae was shown to improve healing and inhibit infections [16].

Instead of using patches and hydrogels, mobile cells were also tested. Nonmotile microalgae coated with

superparamagnetic Fe<sub>3</sub>O<sub>4</sub> NPs were steered directly to the desired location with magnetic fields [10]. Other approaches utilize inherent mobility of microalgae — not only to deliver O<sub>2</sub> to the target site but also to deliver other useful substances (e.g. heparin) and to improve mixing [18]. The generally high biocompatibility of microalgae was further improved by cloaking them in membranes of red blood cells [3]. Even dead microalgae demonstrated to be useful since chlorophyll works similar to light-absorbing ‘photosensitizers’ utilized in conventional photodynamic cancer therapy [3] in that they both donate electrons to O<sub>2</sub> upon light excitation, forming reactive oxygen species (ROS).

### Applications based on photosynthetically generated electrons

Photosynthetic organisms produce excessive electrons under certain conditions. When exposed to high light or low CO<sub>2</sub>, an imbalance between generation of electrons and reduction of NADP<sup>+</sup> occurs. If unaddressed, those excess electrons leak out of the chain and react with O<sub>2</sub>, forming ROS that damage cell components [19]. Therefore, exporting mechanisms for excess electrons exist, which differ in detail between the photosynthetic lineages (Figure 1): eukaryotes mostly rely on NADPH oxidases, while prokaryotes rely on protein nanowires (type IV pilus) located at the plasma membrane [19,20]. Extracellular electrons rapidly react with the environment, either forming ROS or reducing metals. Such photosynthetically generated electrons are used in several applications.

### Biological photovoltaic system

Several types of electrogenic devices exist, which are categorized by the type of organism employed. Photosynthetic or symbiotic microbial fuel cells (PMFCs) use either photoheterotrophic organisms alone or a consortium of both heterotrophic and photoautotrophic organisms to generate electricity using light. These approaches either require heterotrophic metabolisms to produce electrons on anodes or external supplementation of electron acceptors such as O<sub>2</sub> on cathodes [21]. In contrast to PMFCs, biological photovoltaic (BPV) systems use only oxygenic, photoautotrophic organisms, which generate electrons via photolysis of water and produce their own electron acceptors in the form of O<sub>2</sub> (Figure 2c) [22].

As exemplified in Figure 2c, a typical BPV device consists of a transparent chamber for oxygenic photosynthetic organisms, a transparent anode (e.g. indium tin oxide-coated polyethylene terephthalate), and a catalytic metal cathode like platinum [20]. In some devices, a soluble electron carrier like K<sub>3</sub>[Fe(CN)<sub>6</sub>] collects electrons from the liquid medium and donates them to the anode, while in other devices, this step is bypassed

by immobilizing cells at the anode in biofilms or hydrogels [23,24]. The electrons flow from the anode through an external circuit to the cathode, creating electricity to power other devices or to be stored in batteries. O<sub>2</sub> and protons produced during photosynthesis diffuse to cathodes, receiving electrons from cathode and forming water. BPVs’ energy output is not yet comparable to Si-based voltaic systems. For improving BPVs, promising approaches include directly extracting electrons from photosystems via exogenous electron mediators (rewired photosynthesis) and employing biogenic anode materials [25,26].

### Biosynthesis of metal nanoparticles

Metal NPs are typically smaller than 100 nm and exhibit unique physical and chemical properties. They are widely utilized in medical diagnosis, wound care, electron microscopy, and electronics fabrication. Traditional synthesis methods, such as chemical reduction, sol-gel, and hydrothermal synthesis, come with environmental hazards and may introduce toxic impurities in NPs.

Biosynthesis of NPs via photosynthetic organisms excludes environmental hazards and improves biocompatibility (Figure 2d) [27]. In the presence of light, metal NPs can be biosynthesized via electron transport chain on thylakoid membranes by photosynthetic organisms [28]. Metal NPs were shown to accumulate in chloroplasts of eukaryote cells exposed to metal ions [29]. While the exact mechanism is still being investigated, electrons donated from electron transport chain on thylakoid membranes can convert metal ions into metal precipitates, eventually forming metal NPs. For instance, administration of HAuCl<sub>4</sub> (or AgNO<sub>3</sub>) to a microalgae or cyanobacteria culture allows biosynthesis of gold (or silver) NPs in sufficient quantities to cause a color shift in these cultures [30,31].

### Applications based on CO<sub>2</sub> capture

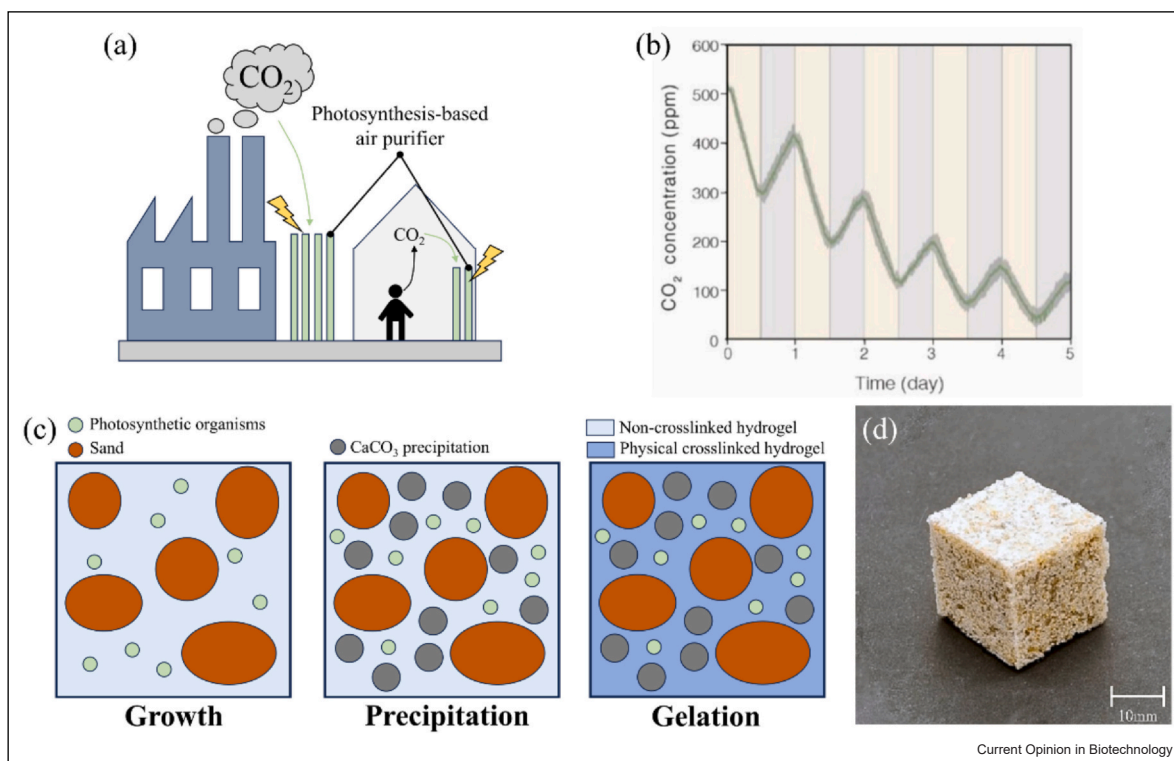
Approximately 25% of yearly anthropogenic C emissions are compensated by forest ecosystems, exemplifying both magnitude of emissions and value of photosynthesis [32]. Although the employment of plants or microalgae inherently adds an element of environmental sustainability to any application, some applications emphasize this aspect more than others.

### Improvement of air quality

Greenhouse gases or pollutants (CO<sub>2</sub>, NO<sub>x</sub>, SO<sub>x</sub>, volatile organic compounds, *etc.*) impact both human health and climate. Poorly ventilated indoor environments often show elevated CO<sub>2</sub> levels compared to outdoor ambient air levels, with measurable effects on human health above 1000–5000 ppm [35]. Physicochemical air cleaning devices (e.g. filters, fuel cells, catalyzers) help lowering emission of pollutants and improving air



Figure 3



Applications based on photosynthetically capturing of CO<sub>2</sub>. **(a)** Concept of photosynthesis-based air purifiers designed to reduce outdoor and indoor CO<sub>2</sub> emissions. **(b)** Five-day monitoring of CO<sub>2</sub> consumption curve of a seven-day old living photosynthetic hydrogel cube under alternating periods of light exposure (beige background) and darkness (gray background) [33]. **(c)** Schematic of CaCO<sub>3</sub> precipitation in sand/hydrogel scaffold with photosynthetic microorganisms. **(d)** Image of a sand/hydrogel scaffold with cyanobacteria [34]. **(b)** With permission from Advanced Materials. **(d)** With permission from Construction and Building Materials.

quality, but they are prone to clogging, difficult to recycle, or require electricity to operate [36].

In addition to being efficient at biofixation of CO<sub>2</sub>, plants and microalgae are able to transform, accumulate, or assimilate a range of other pollutants (Figure 3a) and are therefore occasionally described (and sold) as 'air purifiers' [37]. Microalgae immobilized in hydrogels enable portability and shape control via 3D printing [38–40] and benefit from improved gas exchange and light penetration, thus improved CO<sub>2</sub> fixation and O<sub>2</sub> production (Figure 3b) [33,41]. The CO<sub>2</sub> capture efficiency of cyanobacteria also increases when grown inside porous 3D ceramics, which provide large effective surface areas for illumination [42]. However, it remains to be seen whether these devices are consumer-friendly and practical enough for wider application. Compared to microalgae, plants have a lower net growth rate but also represent a low-maintenance-cost option suitable for private use. The superior productivity of microalgae unfortunately manifests in higher maintenance costs, ranging from 300 to 50 000 \$ per year for a household or public photobioreactor [43].

### Photosynthesis-assisted living building materials

Cement production contributes 7% to global anthropogenic CO<sub>2</sub> emissions due to sintering of limestone and clay [44]. Hence, eco-friendly concretes are being explored, for example, via microorganism-induced calcium carbonate precipitation (MICP). MICP often uses ureolytic bacteria to precipitate CaCO<sub>3</sub> from Ca<sup>2+</sup> ions for biogenic concrete [45]. However, unfavorable NH<sub>3</sub> gas is released in this process, and the low viability of ureolytic bacteria in high-pH environments hinders long lifespan.

Photosynthetic microorganisms are explored to fabricate living building materials (LBMs) that can grow and self-heal. In this case, cells import HCO<sub>3</sub><sup>−</sup> to concentrate CO<sub>2</sub> (Figure 1) and export OH<sup>−</sup>, raising pH to alkaline levels and promoting CaCO<sub>3</sub> precipitation without NH<sub>3</sub> emissions (Figure 3c) [46]. The carbon source for CaCO<sub>3</sub> precipitation can also originate from atmospheric CO<sub>2</sub>, omitting HCO<sub>3</sub><sup>−</sup> addition, and improving environmental sustainability of LBMs [34]. Cyanobacteria-induced CaCO<sub>3</sub> precipitation can mineralize and toughen LBMs, as shown with sand/gelatin LBM containing cyanobacteria (Figure 3d). The embedded microorganisms

may also endow materials with regenerative properties, sealing cracks through biomineralization, with 30-day viability within the scaffold [46].

### Applications based on photosynthetically produced carbohydrates

Carbohydrates derived from photosynthesis have been essential to humans as a source of food, building materials, and clothing since ancient times. Recently, carbohydrates are explored to fabricate bioplastics based on chemically modified cellulose, gelatinized starch, or polyhydroxyalkanoate, emerging as sustainable and biodegradable alternatives of petrochemical plastics. Since bioplastics produced by photosynthetic organisms were reviewed elsewhere [47], we focus instead on photosynthetically produced carbohydrates used for light-responsive polymer remodeling and for waste treatment.

Mechanical properties of materials often deteriorate with time due to degradation and fatigue. Carbohydrates generated via photosynthesis can help to remodel and enhance materials' stiffness (Figure 4a). In a recent photosynthetic living material, glucose locally released from chloroplasts was used to crosslink and strengthen a polymer matrix when illuminated. Hydroxyl groups (-OH) from glucose could interact with isocyanate groups (-NCO) in the hydrogel to form strong urethane linkages (-NH-CO-O-) (Figure 4b) [48]. Alternatively, glucose can be converted into gluconolactone by glucose oxidase (GOx), introducing reactive carbonyl-group (-C=O) groups. These can polymerize with hydrogel polymers containing primary amine groups (-NH<sub>2</sub>) such as poly(aminopropyl methacrylamide) [49], facilitating a living material that strengthens and self-repairs via CO<sub>2</sub> fixation in the presence of light.

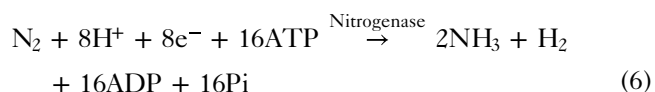
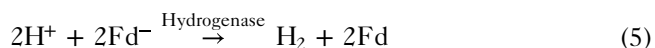
Carbohydrate production by photosynthetic organisms is also used in bioreactors for wastewater treatment. Cattle manure leachate (CML) represents a biodegradable type of wastewater with organic pollutants. Methanogens can use nutrient-rich CML as substrate for CH<sub>4</sub> production via anaerobic digestion while biodegrading organic pollutants. However, the efficiency of hydrolysis, acidogenesis, acetogenesis, and methanogenesis are limited due to unfavorable low-C and high-N concentrations in CML [50]. Anoxygenic phototrophic purple nonsulfur bacteria [51] can be employed to assist in anaerobic digestion of methanogens in bioreactor devices (Figure 4c) indirectly through photosynthesis, producing carbohydrates and shifting the C:N ratio to more favorable levels. The production rate of CH<sub>4</sub> hereby directly correlates with illumination [52].

### H<sub>2</sub> production

H<sub>2</sub> is discussed as a clean energy carrier, but its large-scale production remains a challenge. Since no naturally

occurring sources of easily extractable H<sub>2</sub> exist in high quantities, finding sustainable methods for its mass production is crucial. Photosynthetic microorganisms can produce H<sub>2</sub> through two separate pathways.

In one pathway, electrons from the photosynthetic light reaction are donated via Fd to the hydrogenase complex (HOX), which directly forms H<sub>2</sub> while consuming H<sup>+</sup> (Figure 1, Reaction 5). However, since HOX is sensitive to oxygen, H<sub>2</sub> production ceases during prolonged photosynthetic activity. Efforts to circumvent this include sulfur deprivation, aiming to suppress PSII activity and thus oxygen generation [53], as well as employing a microalga mutant strain that decreases oxygen generation via a deficient cyclic electron flow and higher respiration activity [54]. Immobilization of cells in materials such as alginate and linen-like glass fibers also strives to increase cell density and shield cells from atmospheric O<sub>2</sub> [55,56]. The second pathway is based on the enzyme nitrogenase employed by N<sub>2</sub>-fixing cyanobacteria. Without a sufficient nitrogen source (e.g. NH<sub>4</sub><sup>+</sup>), N<sub>2</sub> is converted under high ATP investment to NH<sub>3</sub>, which releases H<sub>2</sub> as byproduct (chemical Reaction 6) [57]. However, neither pathway currently produces H<sub>2</sub> in sufficient quantities allowing scalability.

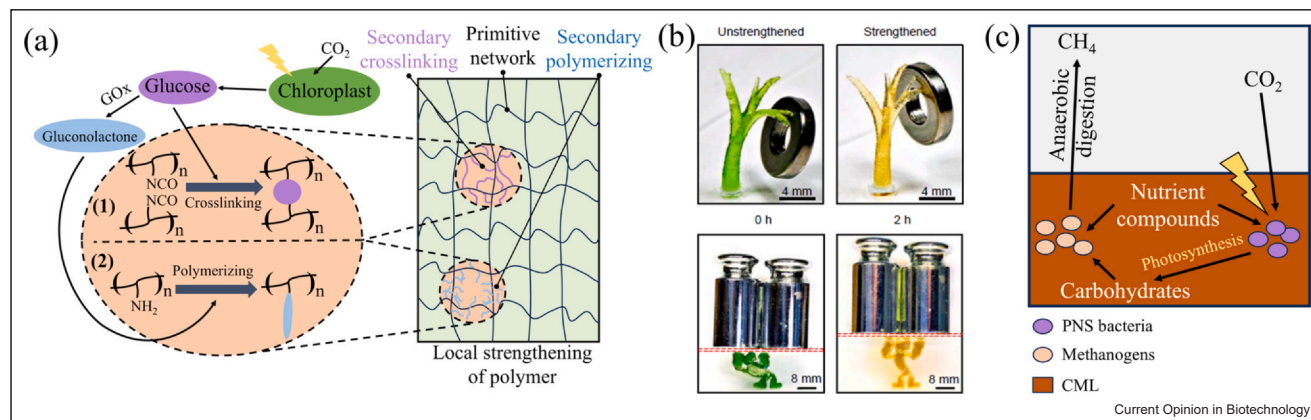


### Conclusion and outlook

In this paper, the recent development of photosynthesis-assisted technologies was summarized, with applications in material fabrication, electricity generation, biomedicine, environmental improvement, or fuel production. Many of these applications share similar challenges that currently hamper their wider use.

- (1) Financial aspects: Similar to plants in greenhouses, providing optimal conditions for microalgae also increases maintenance costs. CO<sub>2</sub> capture — associated with most applications — does not come with immediate monetary value, so it is rarely included in cost calculations. This might partially explain why only high-value high-biomass products such as pigments have gained traction in industry, while low-value high-biomass products such as biofuels remain unestablished [58]. Several options to improve efficiencies exist. Genetic engineering led to more productive strains, albeit within the limits of respective biological systems [59]. Another approach would be to combine the manifold applications into symbiotic, synergistic industries, for example, photosynthesis-assisted wastewater treatment followed by cell extraction for bioplastics.

Figure 4



Applications based on photosynthetically produced carbohydrates. **(a)** Schematic showing glucose produced by chloroplasts promoting cross-linking/polymerizing of hydrogels for increased structural integrity in hydrogels. **(b)** Images demonstrating the enhanced structural stability of chloroplast-containing 3D hydrogels when reinforced with photosynthesis-produced glucose [48]. **(c)** Schematic of photosynthesis-assisted conversion of manure waste into CH<sub>4</sub>. PNS bacteria, purple nonsulfur bacteria.

**(b)** With Permission from Proceedings of the National Academy of Sciences.

- (2) Ensuring performance stability and lifetime: Most industrial applications desire reliable, reproducible, and steady long-term performance difficult to achieve with living organisms that continuously adjust their metabolism to their environment. The reliance of photosynthesis on illumination can serve as a control feature, but its variability needs to be considered (e.g. wound patches under clothing or opaque wastewater). Most applications would likely benefit from bioreactor-like setups that allow continuous addition of nutrients and removal of biomass. The low lifetime of some photosynthetic materials and devices described here highlights the requirement of either more durable organisms or more sophisticated water and nutrient delivery systems.

Continuing the current trend of increasing interdisciplinary collaboration, including biologists, engineers, and chemists, will hopefully lead to solutions that assert themselves in the market.

### CRedit authorship contribution statement

**Fan Jiang:** Conceptualization, Writing – original draft preparation, Visualization. **Friedrich Hans Kleiner:** Conceptualization, Writing – original draft preparation, Supervision. **Marie-Eve Aubin-Tam:** Conceptualization, Writing – review & editing, Supervision, Funding acquisition.

### Data Availability

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

### 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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- of special interest
- of outstanding interest

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