Photosynthesis is a biological process of energy conversion from solar radiation to useful organic compounds for the photosynthetic organisms themselves. It, thereby, also plays a role of food production for almost all animals on the Earth. The utilization of photosynthesis as an artificial carbon cycle is also attracting a lot of attention regarding its benefits for human life. Hydrogen and biofuels, obtained from photosynthetic microorganisms, such as microalgae and cyanobacteria, will be promising products as energy and material resources. Considering that the efficiency of bioenergy production is insufficient to replace fossil fuels at present, techniques for the industrial utilization of photosynthesis processes need to be developed intensively. Increase in the efficiency of photosynthesis, the yields of target substances, and the growth rates of algae and cyanobacteria must be subjects for efficient industrialization. Here, we overview the whole aspect of the energy production from photosynthesis to biomass production of various photosynthetic microorganisms.

Key Words: algae; biofuel; carbohydrate; cyanobacteria; hydrogen; lipid; photosynthesis

Abbreviations: ACP, acylcarrier protein; CCM, carbon-concentrating mechanism; DHA, docosahexaenoic acid; EPA, eicosapentanoic acid; PS, photosystem; TG, triacylglycerol

Introduction

There is a growing interest in developing technology for renewable energy production to deal with the shortage of fossil fuel and with global warming caused possibly by the increase in carbon dioxide atmospheric concentration. Photosynthesis-biological energy conversion of solar radiation to organic compounds has been considered as one of the appropriate methods to resolve these problems (Radakovits et al., 2010; Santos-Merino et al., 2019; Stephens et al., 2010; Stephenson et al., 2011). Photosynthesis is distributed in a wide variety of organisms, such as terrestrial higher plants, seaweeds, microalgae, and cyanobacteria. Though some oil plants, such as *Jatropha* and *Eucalyptus*, have been investigated as candidates for biomass production as renewable energy sources, they might compete with crops in the agricultural field (Azócar et al., 2010). In this respect, since microalgae have been indicated to grow faster than crops, microalgae have been considered to be appropriate organisms for biomass production as energy resources (Chisti, 2008; Wijffels and Barbosa, 2010). Though the word “microalgae” indicates eukaryotic organisms, and does not involve cyanobacteria in basic sciences, we do not separate them so clearly here in this paper, because of their similarity in ecological status especially in technology. In any case, biomass production with microalgae has been investigated intensively (Benedetti et al., 2018; Jones and Mayfield, 2012; Kiyota et al., 2014).

However, it may still take time to achieve industrialization, not only because of the cost of the algal production, but also due to the amount involved. Mass cultivation of microalgae has been due to solar radiation so far, because the solar radiation received by the Earth is enormous. Indeed, solar energy to the Earth on an annual basis is estimated to be about $1.0-1.2 \times 10^{17}$ W, while the annual global energy consumption by mankind is about $1.4-1.5 \times 10^{13}$ W (Blankenship et al., 2011). The amount of solar radiation seems to be much higher than the energy consumed by human activity at first glance. It should be noted, however, that the real amount of solar energy which is incident on the Earth’s surface is much lower due to absorption and reflection during travel through the atmos-
Photosynthetic Energy Conversion from Light Capture to ATP and NADPH Production on Thylakoid Membranes

Photosynthesis is essentially a conversion process of light energy to a biologically available form of chemical energy (Blankenship et al., 2011), in which light energy is used to produce high-energy phosphate bonds in ATP and reduced compounds, such as NADPH and reduced ferredoxin (Fd), through photosynthetic electron transport. This results in inorganic carbon being incorporated into organic compounds, such as carbohydrates, lipids and proteins, by way of phosphate esters. Thus, photosynthesis mainly involves two processes: energy conversion of light and carbon incorporation into organic compounds.

Oxidogenic photosynthetic organisms have two reaction centers in integral membrane protein complexes which are embedded in the thylakoid: O$_2$-evolving photosystem II (Ikeuchi, 1992; Shen, 2015), and Fd-reducing photosystem I in the order of electron transfer known as the Z scheme (Nelson and Ben-Shem, 2004). Under illumination, electrons are released from PSII and PSI, and linear electron transport from PSII to PSI occurs. In PSII, protons are released by the splitting of water in the lumen, while PSI donates electrons finally to NADP$^+$ via Fd. A gradient of protons, which are pumped into the thylakoid lumen during the electron transport, is used for ATP synthesis by F$_0$F$_1$-ATPase (Hisabori et al., 2003). Cyclic electron flow around PSI also operates for ATP production (Nawrocki et al., 2018). Rubisco activase activates Rubisco by the release of CO$_2$, and this is then utilized for photosynthesis.

Photosynthesis is distributed in a wide range of organisms, including prokaryotes and eukaryotes. Most photosynthetic bacteria show anoxygenic photosynthesis containing only one photosystem. On the other hand, all eukaryotic photosynthetic organisms, and a group (phyllum) of prokaryotes-cyanobacteria perform oxygenic photosynthesis. In the eukaryotic cells, chloroplast, the origin of which is now believed to be an ancestor of extant cyanobacteria in endosymbiosis theory, is the compartment of photosynthesis (Stiller, 2007). The endosymbiotic cell evolved to groups of Glaucoaphya and Rhodophyta, as the early organisms of photosynthetic eukaryotes, and then, further, to green plants (Keeling, 2010). On the other hand, engulfment of phototrophic eukaryotes (red or green algae) by heterotrophic eukaryotes might have happened on eukaryotic photosynthetic cells to be secondary endosymbiosis. Several groups of microalgae might have evolved to be Cryptophyta, Haptophyta, Stramenopiles, Dinophyta, Euglenophyta, and so on. Therefore, microalgae are now extremely diverse, including more than 35,000 species (Larkum et al., 2012).

While the mechanism of ATP and NADPH production in oxygeneic photosynthesis is very similar among the species, there is a remarkable diversity in antenna protein complexes. Light harvesting chlorophyll (Chl)-binding protein (LHCP) complexes contain Chl $a$ and $b$ in green plants, and Chl $a$ and $c$ in the organisms developed from secondary endosymbiosis, such as diatoms and brown algae (Büchel, 2015). Instead of LHCP, cyanobacteria and Rhodophyta contain phycobilisomes which are composed of blue and red pigment-binding proteins: phycocyanin and phycoerythin (Li et al., 2019; Pagels et al., 2019). Recently Chl $d$ (Ohashi et al., 2008) and Chl $f$ (Nürnberg et al., 2018) were also discovered. Carotenoids, consisting of carotenes and xanthophylls, also play roles in light capture and protection from extremely high light intensities in algae. The xanthophyll cycle, including pigments such as zeaxanthin, diadinoxanthin, and diatoxanthin, functions to release excessive light energy under high light conditions in many algae (Latowski et al., 2011), while alloxanthin, instead of the usual xanthophyll cycle pigments, seems to be involved in photoprotection in the cryptophyte Guillardia theta (Funk et al., 2011).

Photosynthetic Carbon Fixation in the First Step

Photosynthetic carbon fixation in cyanobacteria and in chloroplast stroma

Using NADPH and ATP produced by photosynthetic electron transport under irradiation, carbon dioxide is incorporated into organic compounds, including starch and lipids, via the Calvin-Benson cycle. The carboxylation reaction catalyzed by Rubisco is one of rate limiting steps in the Calvin-Benson cycle under conditions of sufficient light intensities and CO$_2$. The rate of carboxylation by Rubisco is very slow with a few CO$_2$ molecules fixed per second. Rubisco concentration in stroma is then, extraordinarily high (almost in the order of mM; the amount corresponds to about a half of that of soluble proteins in chloroplast (Ellis, 1979)) to catch up with the rate of photosynthesis. Thus, Rubisco may be the most abundant protein on the Earth.

The Calvin-Benson cycle is activated by various environmental factors during photosynthesis (Buchanan, 1991). Several enzymes involved in this cycle are activated by light via high stromal pH and via reducing equivalents generated by photosynthetic electron transport (Buchanan, 1991; Geigenberger et al., 2005). The activity of Rubisco is regulated by a special regulator: Rubisco activase (Mueller-Cajar and Whitney, 2008; Portis et al., 2008). Rubisco activase activates Rubisco by the release
of an inhibitor 2-carboxyarabinitol 1-phosphate, which has been produced in the dark, from the catalytic site of Rubisco. Rubisco activase is activated by a high ATP/ADP ratio and reduced state of thioredoxin, which are generated in the light. Fructose-1,6-bisphosphatase, sedoheptulose-1,7-bisphosphatase, NADP-dependent glyceraldehyde-3-phosphate dehydrogenase, and phosphoribulokinase are also activated by reduced thioredoxin (Buchanan, 1991; Nikkanen and Rintamäki, 2019).

**Further metabolism of fixed carbon into final products**

Organic carbon fixed by the Calvin-Benson cycle is further metabolized to be incorporated into cellular components, such as carbohydrates, lipids, and proteins. Carbohydrates synthesized in photosynthesis show a variety depending on the organisms: starch in Chlorophyta, Cryptophyta, and Dinophyta, mannitol in the green alga *Chlorella kessleri* 11 h under ordinal photoautotrophic growth conditions in the authors’ laboratory.

![Table 1. The outline of ingredient composition in a green alga *Chlorella* cell as an example.](image)

| Content     | Amount (pg per a cell)* |
|-------------|-------------------------|
| Dry weight  | 14–16                   |
| Carbon atom | 7–9                     |
| Nitrogen atom | 0.4–0.9               |
| Chlorophyll | 0.9–1.2                 |
| Carbohydrate | 1.5–4.0                |
| Protein     | 7.5–8.0                 |
| Lipid       | 1.5–4.5                 |

*The values were obtained with *Chlorella kessleri* 11 h under ordinal photoautotrophic growth conditions in the authors' laboratory.

The elongation of the carbon chain ceases at C16 and C18 fatty acids in cyanobacteria and green plants, while in some microalgae, such as diatoms, the elongation can be continued to produce C20 and C22 fatty acids, including commercially valuable eicosapentanoic acid (EPA) and docosahexaenoic acid (DHA). The elongation to C20 or C22 fatty acids is catalyzed by fatty acid elongase, using acy-CoA, but not acy-ACP, as a substrate in diatoms (Zulu et al., 2018).

Glycerol 3-phosphate is converted to lisophosphatidic acid, followed by esterification with ACP-fatty acids into diacylglycerol and then triacylglycerol (TG) (Sato and Wada, 2009). Unsaturation of the acyl residues in the lipid molecules is catalyzed by desaturases, each of which reacts with a specific bond of acyl residue (e.g., ω-3 and ω-6 desaturases synthesize ω-3 and ω-6 fatty acids, unsaturated fatty acids with a double bond (C=C) at the 3rd and 6th C from the methyl end, respectively).

Glutamine is synthesized by glutamine synthetase (GS) using glutamate, ammonia, and ATP, and the NH₂-moieties of the γ-amido group is then transferred to 2-oxoglutarate by GOGAT, giving rise to glutamate (Fernandez and Galvan, 2007; Muro-Pastor et al., 2005). Other amino acids are synthesized by aminotransferases. Amino acids produced during photosynthesis are subsequently converted to proteins.

**Regulation of photosynthetic carbon metabolism**

Carbon metabolism in macromolecular synthesis is affected by environmental factors such as light, temperature and nutrients (Jamers et al., 2009; Weckwerth, 2011). Under light irradiation, starch synthesis is activated by the reduction of regulatory thioles of ADP glucose pyrophosphorylase by thioredoxin or NADPH-dependent thioredoxin reductase C, while lipid synthesis is stimulated by the reduction of those of acetyl-CoA carboxylase and monogalactosyldiacylglycerol synthase by thioredoxin in green plants (Dietz and Pfannschmidt, 2011). Nutrient stresses and high CO₂ conditions induce starch accumulation in green algae such as *Chlorella* (Brányiková et al., 2010; Izumo et al., 2007). TG is accumulated in starchless mutants of *Chlamydomonas* by nitrogen deficiency (Li et al., 2010; Wang et al., 2009). Sulfur deficiency induces TG synthesis even in the wild type of *Chlorella* and *Parachlorella* (Mizuno et al., 2013).

**Efficiencies of Microalgal Photosynthesis and Growth**

Even though several candidate organisms can be identified for energy and biomass production with microorganisms, there exist difficult problems to be solved regarding the industrialization. Economic and scale barriers for production must be overcome in comparison with fossil fuels. Then, we must improve the efficiency and the yield of photosynthesis and growth of the photosynthetic microorganisms to meet the demand of energy and materials.

On the efficiency of energy conversion in photosynthesis, the quantum requirement, i.e. the quantum absorption per mole oxygen evolved, is 8, indicating that 8 photons are required for 1 molecule of O₂ evolved (nearly equal
for CO₂ fixed) during photosynthesis (Emerson and Arnold, 1932; Grobbelaar, 2010). The photosynthetic reaction caused by photon absorption inside protein complexes proceeds nearly 100% without energy loss. However, the ratio of irradiated light to photosynthetic oxygen evolution is commonly about 15–20 in growing cells. The efficiencies of light utilization are now close to 10% under red light. Improvement is still required for industrialization (Nakajima et al., 2001). Using modified Chl may extend the range of solar light absorption (Chen and Blankenship, 2011). Actually, Chl d enables the cyanobacterium Acaryochloris to use infrared light that is not absorbed by Chl a.

Alternatively, one can notice that Rubisco is one of the most important targets in improving the efficiency of photosynthesis (Peterhansel et al., 2008). This enzyme catalyzes the reaction between RuBP and O₂, in addition to CO₂, that causes a loss of photosynthetic energy through photorespiration at atmospheric O₂ concentration. Genetic engineering studies aimed at increasing the activity and specificity of Rubisco have been carried out, though the activity and specificity have shown an inverse relationship (Cai et al., 2014). The models of trade-offs in Rubisco catalysis were examined, using a data set from ~300 organisms (Flamholz et al., 2019). Such a survey of Rubisco from higher plants to algae concerning activities and specificities, may help to identify promising candidates with both high activity and specificity. However, actually, it seems to be difficult to find Rubisco with high activities and a high specificity (Flamholz et al., 2019), as suggested by Savir et al. (2010). For enhancement of the biomass production by genetic engineering, the most potential strategies may be: (1) cotransduction of Rubisco with a high activity but relatively low specificity from cyanobacteria, such as Synechococcus sp. PCC 6301, and carbon concentrating mechanisms (CCM); or (2) overexpression of Rubisco with a high specificity but relatively low activity from Rhodophyta, such as Galderia sulfuraria. Genetic engineering studies aimed at increasing the rate of photosynthesis by overexpression of Rubisco have also been reported. Overexpression of $rbcL$S from Synechococcus elongatus PCC 6301 in S. elongatus PCC 7942, which has Rubisco with a sequence identical to that of S. elongatus PCC 6301, increased in vitro Rubisco activity and isobutyraldehyde production two fold, while it did not cause an increase in oxygen evolution rate (Atsumi et al., 2009). In Synechocystis PCC 6803 overexpressing $rbcL$S, in which the expression of the indigenous $rbcL$S genes were stimulated by a strong promoter, the Rubisco content, growth rate, and rate of photosynthesis were increased (Liang and Lindblad, 2017). Also, an improvement of energy requirement in CO₂ fixation pathways by designing the carbon fixation pathways by synthetic biology has been proposed (Bar-Even et al., 2010).

Another important step for biomass production is the efficiency of the CO₂ supply from the outside of the cell to the active site of Rubisco. When microalgae and cyanobacteria are grown under 2–5% CO₂, they show a low affinity of photosynthesis to CO₂ concentrations. The affinity is raised in the cells grown under ordinary air conditions, indicating that CCM is inducible under limiting CO₂ conditions, such as atmospheric CO₂ concentration. CCM in microalgae and cyanobacteria, which is mediated by inorganic carbon transport system(s) and carbonic anhydrase (Aizawa and Miyachi, 1986), has been elucidated substantially (Rae et al., 2013; Raven et al., 2008).

So, how much does the rate of photosynthesis affect cell growth? Some unicellular microalgae, such as Chlorella (Tsuzuki et al., 2019), can proliferate about 2–10 times a day under appropriate conditions, and some cyanobacteria seem to be a little faster (e.g., Synechococcus elongatus PCC 11801 (Jaiswal et al., 2018)). Under appropriate conditions, Chlorella cells divided when the total amount of carbon fixed by photosynthesis was doubled, suggesting that there are no other limiting steps (Tsuzuki et al., 2019).

**Biotechnology for Bioenergy Production by Photosynthesis**

Because photosynthesis is a complex mechanism, and because photosynthetic microorganisms show a huge biological diversity, various projects to obtain energy can be conducted from various sources of the organisms.

Electrical energy can be captured from the organisms in the light by way of microbial fuel cells (MFCs) (Rosenbaum et al., 2010). MFCs are bioelectrochemical systems for electric power generation based on the exploitation of biocatalytic reactions with active microbial cells. Electrons are liberated from substrates through biocatalysts at an anode, pass through an external load as an electric current, and combine with a cathodic electron acceptor through electrocatalytic or biocatalytic reactions.

Hydrogen is a clean energy resource which does not generate carbon dioxide in combustion, and it is expected that hydrogen can be applied to fuel cells and hydrogen engines. Biological hydrogen production performed by photosynthesis is direct biophotolysis of water using microalgae and cyanobacteria (Dubini and Ghirardi, 2015; Eroglu and Melis, 2011). Hydrogen is generated by nitrogenase, consuming ATP as energy, or hydrogenase. Under anaerobic conditions, the primary products of photosynthesis, viz. reduced ferredoxin, NADPH, and ATP, could be utilized for hydrogen production in green microalgae, such as Chlamydomonas, with hydrogenase linked with photosystem I, as they do not have nitrogenase (Eroglu and Melis, 2011; Kruse and Hankamer, 2010). Cyanobacteria can also generate hydrogen either with hydrogenase or nitrogenase (Sakurai and Masukawa, 2007). In nitrogen fixing cyanobacteria (i.e., Anabaena), hydrogen is produced by nitrogenase. However, these species of cyanobacteria possess two different kinds of [NiFe] hydrogenases with different properties and functions, one is hydrogen-uptake [NiFe] hydrogenase and the other is bidirectional hydrogenase, and the former catalyzes a hydrogen degrading reaction with reducing cyt b. Inactivation of the hydrogen-uptake hydrogenase leads to a significant increase in the hydrogen production activity (Masukawa et al., 2002), and hydrogen-related reactions, including gene expression, are strongly suppressed under aerobic conditions (Lubner et al., 2011). Then, direct biophotolysis can operate for short periods of time upon...
the onset of illumination (a few minutes), before the accumulating oxygen inactivates the hydrogen-production process. Hydrogen evolution continues only so long as the partial pressure of oxygen remains low (Martin and Frymier, 2017). In this respect, genetic engineering for the introduction of oxygen-resistant hydrogenase and for the construction of linkage between photosystem I and hydrogenase have been investigated (Martin and Frymier, 2017).

Organic compounds are other candidates for energy and biomass production. Ethanol is the most convenient liquid as a fuel and gasoline enhancer. Production of ethanol for biofuel has increased in some countries through fermentation from starch and cellulose (Radakovits et al., 2010). Ethanol could be synthesized in *Chlamydomonas* cells in the night (Hirano et al., 1997) and in gene-manipulated cyanobacteria (Radakovits et al., 2010; Santos-Merino et al., 2019). Ethanol could be synthesized in *Chlamydomonas* cells through degradation and fermentation of intracellular starch. In this process, starch is synthesized under light condition, and intracellular starch is converted to ethanol through digestion and fermentation under dark and anaerobic conditions (Hirano et al., 1997). In cyanobacteria, ethanol is produced under aerobic photosynthetic conditions in strains, in which pyruvate decarboxylase and aldehyde dehydrogenase genes are introduced (Deng and Coleman, 1999). Bio-hythane (mixture of H۲ and CH۴ produced from biological resources via biological processes) is also produced from microalgal biomass (e.g., *Chlorella* and *Microcystis*) via a two-stage fermentation (H۲ and CO۲ synthesis during dark fermentation and then CH۴ and CO۲ production during anaerobic digestion) (Ghimire et al., 2017).

Microalgae are now concerned as a biodiesel platform on the TG or wax ester production because they may not compete with the crops. The species which are known to accumulate higher content of lipids are diatoms, *Nannochloropsis*, *Euglena*, and some green algae such as *Dunaliella* (Inui et al., 2017; Larkum et al., 2012; Scott et al., 2010). In *Chlamydomonas* and *Chlorella*, mutants and wild-type cells can accumulate TG under stress conditions, as was mentioned above (Li et al., 2010; Mizuno et al., 2013). In cyanobacteria, production of free fatty acids, fatty alcohols and aldehydes, hydrocarbons, and wax esters, which are derived from fatty acyl-ACP, have been engineered (Knot et al., 2018). In particular, free fatty acid production has been intensively investigated, using engineered fatty-acids secreting strains (e.g., Kaczmarzyk and Fulda, 2010; Liu et al., 2011; Ruffing, 2013a, 2013b, 2014).

Hydrocarbon is a storage lipid in *Botryococcus braunii*. This green alga has been characterized by its ability to synthesize and accumulate hydrocarbons. It produces triterpenoid botryococenes, a potential fuel molecule that requires minimal refining (Metzger and Largeau, 2005). *Pseudochoricystis* produces hydrocarbons of shorter carbon chains, such as heptadecene, heptadecane and eicosadienes as major hydrocarbons, and genetic engineering is applicable for this strain (Satoh et al., 2010; Imamura et al., 2012). *Emiliania huxleyi* and *Gephyrocapsa oceanica*, marine planktonic algae, produce normal alkenones (C۱۱ to C۳۳) (Ono et al., 2009).

In addition, commercially-valuable compounds such as EPA and DHA have also been considered as a by-product of biofuels. β-carotene from *Dunaliella* and astaxanthin from *Hematococcus* might be other candidates for by-products (Work et al., 2011). Because of the extensive research on biofuel production, many reviews including a list of lipid content of various microalgae and also mass culture systems have appeared recently (see Harun et al., 2010; Quintana et al., 2011; Radakovits et al., 2010).

**Conclusion**

There still exist several challenges to overcome in order to achieve hydrogen and biofuel production on a commercial base: the selection of algal species, culture and production methods using open pond or photobioreactors, and the extraction method of oil. In order to produce a sufficient amount of hydrogen or biofuels along with a low cost, better algal strains with or without gene manipulation, better optimized culture conditions, and more powerful culture systems, are still required for industrialization. Combining each improvement will help to facilitate that goal. Although non-biological systems on the energy conversion are expected to be developed in the future, the self-supply of biomaterials would be an advantage due to the multiplication of organisms. Therefore, the development of energy conversion using photosynthetic microorganisms must be one of the most promising technologies.

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