Photosynthesis in Nature: A New Look

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1 Introduction

Photosynthesis is a fundamental process on the Earth's surface that can convert the sunlight energy to chemical energy that can be used by essentially all forms all life (Komissarov 2003; Krauß 2003). The outstanding English chemist Joseph Priestley

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in 1771 and 1772 firstly hypothesised on photosynthesis that plants can restore to the air whatever breathing animals and burning candles remove. Jan Ingenhousz in 1779 showed that light is essential to the plant process that somehow purifies air fouled by candles or animals. Based on the experiments, he concluded that plants are dependent on light and their green parts for nutrients and energy.

The experiments conducted by J. Senebier and N. Th. de Saussure revealed that the initial substances of photosynthesis are carbon dioxide (CO_2) and water (H_2O) (de Saussure 1804; Bay 1931). It has been shown by de Saussure (1804) that H_2O is a reactant in photosynthesis. The CO_2 cleavage hypothesis readily accounted for the deceptively simple overall photosynthesis equation ($CO_2 + H_2O + h\upsilon \rightarrow CH_2O + O_2$) (de Saussure 1804). The C:2H:O proportion in the reaction made people assumed that carbon from the photodecomposition of CO_2 can recombine with the elements of water. In 1905 the British scientist F. Blackmann discovered that photosynthesis consists of a light reaction, which is rapid, and a slower dark reaction (Blackman 1905; Blackman and Matthaei 1905). In 1924, O. Warburg and T. Uyesugi explained the result of Blackman as showing that photosynthesis has two classes of reactions: light and dark reactions (Warburg and Uyesugi 1924). In 1922 the German Scientists O. Warburg and E. Negelein revealed the minimum quantum requirement (i.e., minimum number of photons) to be 3–4 per oxygen molecule evolved during the overall process of photosynthesis (Warburg and Negelein 1922). This was later shown to be in error by a factor of 2–3 (Govindjee 1999). Warburg then was awarded the 1931 Nobel Prize in Physiology and Medicine for his discoveries concerning respiration. In 1937 the British scientist R. Hill provided the biochemical proof of the existence of these light and dark phases (Hill 1937, 1939).

In 1931 the American microbiologist van Niel showed that the photosynthetic processes in various pigmented organisms can be interpreted as special cases of a general process expressed as follows (van Niel 1931):

$$2H_2A + CO_2 \xrightarrow[\text{[Radiant energy]}]{\text{Pigments and}} CH_2O + H_2O + 2A \tag{1.1}$$

where light energy is used to photodecompose a hydrogen donor (H_2A) whilst carbon dioxide is reduced anaerobically to cell substance in the dark, using enzymatic reactions (van Niel 1931). According to this generalization, H_2A is water in the case of plants, whilst H_2A is H_2S (or $Na_2S_2O_3$, Na_2SO_3, S, molecular hydrogen, organic substrates and so on) in green and purple sulfur bacteria. Therefore, O_2 is the by-product of plant photosynthesis and elemental sulfur or other compounds are the by-products of bacterial photosynthesis (van Niel 1931, 1936; Roelofsen 1935; Muller 1933).

van Niel in 1941 postulated that the photoinduced reaction in the photosynthetic processes of green bacteria, purple bacteria, and green plants represents, in all cases, a photodecomposition of water (van Niel 1941). The scientist Hill then demonstrated that isolated chloroplasts can evolve oxygen but cannot assimilate CO_2 (Hill 1939, 1951). In 1941, two Soviet and several American scientists discovered that oxygen released by higher plants and algae in photosynthesis is originated from H_2O and not from CO_2 (Ruben et al. 1941; Vinogradov and Teĭs 1941).

Calvin and his colleagues (A. Benson and J. Bassham) during the period of 1947–1956 depicted the mechanism that carbon travels through a plant during photosynthesis, starting from its absorption as atmospheric carbon dioxide to its conversion into carbohydrates and other organic compounds (Bassham et al. 1956; Calvin 1956). They showed that sunlight can act on chlorophyll in a plant to fuel the production of organic compounds, rather than on CO_2 as was previously believed. Calvin was then awarded the Nobel Prize in Chemistry in 1961 for his Calvin cycle (sometimes termed as Calvin-Benson-Bassham Cycle).

Since then, a lot of studies have been conducted on photosynthesis regarding release of electrons from chlorophylls, characterization of the primary reaction centers of photosystems (PSI and PSII), occurrence and formation of chlorophyll dimer in PSI and PSII, functions and roles of PSI and PSII, endogenous formation of hydrogen peroxide (H_2O_2) in photosynthetic cells, release of O_2, and so on (Hill 1937, 1939; van Niel 1931; Bach 1894; Arnon 1949, 1959, 1961, 1971; Mehler 1951; Asada et al. 1974; Chance et al. 1979; Halliwell 1981; Holland et al. 1982; Boekema et al. 1987, 2001 Shipman et al. 1976; Hynninen and Lötjönen 1993; Krauss et al. 1993; Krauß et al. 1996; Shubin et al. 1993; Golbeck 1994; Kruip et al. 1994; Boussaad et al. 1997; Brettel 1997; Wilhelm et al. 1996, 1997, 1999; Klukas et al. 1999; Halliwell and Gutteridge 1999; López-Huertas et al. 1999; Stewart et al. 2000; Jordan et al. 2001; Baker and Graham 2002; Ben-Shem et al. 2003; Catalan et al. 2004; Dashdorj et al. 2004; Germano et al. 2004; Diner and Rappaport 2002; del Río et al. 2006; Li et al. 2006; Krasnovsky 2007; Krieger-Liszkay et al. 2008; Rappaport and Diner 2008; Amunts et al. 2010; Müller et al. 2010; Nilsson Lill 2011; Umena et al. 2011).

Moreover, release of O_2 during photosynthesis still remains under debate because it is considered to be originated either from H_2O (Dashdorj et al. 2004; Germano et al. 2004; Rappaport and Diner 2008; Müller et al. 2010; Takahashi et al. 1987; Periasamy et al. 1978) or from H_2O_2 (Komissarov 1994, 2003; Bach 1893; Velthuys and Kok 1978; Asada and Badger 1984; Asada and Takahashi 1987; Mano et al. 1987; Renger 1987; Anan'ev and Klimov 1988; Bader and Schmid 1988, 1989; Schroeder 1989; Schröder and Åkerlund 1990; Miyake and Asada 1992; Bader 1994, 1995; Yin et al. 2006; Mostofa et al. 2009; Kuznetsov et al. 2010; Bernardini et al. 2011; Mostofa et al. 2009). The scientist Bach has been the first to show that plants actively accumulate H_2O_2 upon illumination (Bach 1894). The major generation sites of reactive oxygen species (ROS) are the PSI and PSII photosystems in chloroplast thylakoids in higher plants. Here, photoreduction of O_2 to H_2O_2 in PSI has firstly been discovered by Mehler (Mehler 1951). Subsequently, the primary reduced product has been identified as the superoxide anion ($O_2^{\bullet-}$), the disproportionation of which can produce H_2O_2 and O_2 (Asada et al. 1974). Recently, H_2O_2 instead of H_2O has been proposed to react with CO_2 in photosynthesis, whereas H_2O_2 is used as an intermediate to release O_2 (Komissarov 1994, 2003; Velthuys and Kok 1978; Mano et al. 1987; Renger 1987; Anan'ev and Klimov 1988; Bader and Schmid 1988, 1989; Schroeder 1989; Schröder and Åkerlund 1990; Miyake and Asada 1992; Bader 1994; 1995; Yin et al. 2006; Mostofa et al. 2009; Kuznetsov et al. 2010; Bernardini et al. 2011). Komissarov (1994, 1995, 2003) has been summarizing on the new hypothesis concerning the photosynthetic reaction, according to which the interaction between CO_2 in air and H_2O_2 in aqueous media (instead of H_2O as for the earlier concept) may form carbohydrate in plants.

Photosynthesis is significantly affected by several factors such as seasonal variation in sunlight and UV radiation (Marshall and Orr 1928; Barker 1935; Jenkin 1937; Rabinowitch 1951; Nielsen 1951, 1952; Aro et al. 1993; Melis 1999; Andersson and Aro 2001; Han et al. 2001; Nishiyama et al. 2001, 2009; Sinha et al. 2001a; Adir et al. 2003; Rastogi et al. 2010; Jiang and Qiu 2011; Sobek et al. 2007; Zhang et al. 2010), occurrence of CO_2 forms (CO_2, H_2CO_3, HCO_3^-, and CO_3^-) (Wong et al. 1975; O'Leary 1981; Cooper and McRoy 1988; Farquhar et al. 1989; Raven and Farquhar 1990; Fogel et al. 1992; Rau et al. 1992; Francois et al. 1993; Raven et al. 1993, 2002; Jasper and Hayes 1994; Laws et al. 1995; Yoshioka 1997; Hu et al. 2012), variations in temperature (Sobek et al. 2007; Mortain-Bertrand et al. 1988; Davison 1991; Wilen et al. 1995; Lesser and Gorbunov 2001; Baulch et al. 2005; Doyle et al. 2005; Yoshiyama and Sharp 2006; Ogweno et al. 2008; Higuchi et al. 2009; Bouman et al. 2010), effects of water stress (drought) and precipitation/rainfall (Munns et al. 1979; Jones and Turner 1978; Matsuda and Riazi 1981; Kaiser 1987; Asada 1992; Hopkins and Hüner 1995; Aziz and Larher 1998; Li and van Staden 1998; Nam et al. 1998; Cornic 2000; Wilson et al. 2000; Lawlor 2002; Velikova and Tsonev 2003; Flexas et al. 2004; Hassan 2006; Liu et al. 2006; Ohashi et al. 2006; Fariduddin et al. 2009), effects of the contents and nature of DOM and POM (Haan 1974; de Haan 1977; Stabel et al. 1979; Jackson and Hecky 1980; Wright 1988; Lindell et al. 1995; Brussaard et al. 1996; Brussaard et al. 2005; Brussaard et al. 2007; Carpenter et al. 1998; Igarashi et al. 1998; Reche et al. 1998; Rengefors and Legrand 2001; Sukenik et al. 2002; de Lange et al. 2003; Hanson et al. 2003; Houser et al. 2003; Druon et al. 2010), variation in nutrient contents (Yoshiyama and Sharp 2006; Martinez and Cerda 1989; Vıllora et al. 2000; Parkhill et al. 2001; Smith 2003; Kaneko et al. 2004; Sterner et al. 2004; Turhan and Eris 2005; Huszar et al. 2006; Liu et al. 2007; Wang and Han 2007; Nõges et al. 2008; McCarthy et al. 2009; Mohlin and Wulff 2009; Achakzai et al. 2010; Bybordi 2010; Tunçtürk et al. 2011), variation in trace metal ions with effects on aquatic microorganisms (Zhang et al. 2010; Crist et al. 1981; Zhou and Wangersky 1985, 1989; Simkiss and Taylor 1989; Xue and Sigg 1990; Tessier and Turner 1995; Sunda and Huntsman 1998; Burda et al. 2003; Koukal et al. 2003; Mylon et al. 2003; Sigfridsson et al. 2004; Berden-Zrimec et al. 2007; Lamelas and Slaveykova 2007; Hopkinson and Barbeau 2008; Lamelas et al. 2009; Pan et al. 2009), effect of salinity or salt stress (Liu et al. 2007; Bybordi 2010; Tunçtürk et al. 2011; Satoh et al. 1983; Ahel et al. 1996; Moisander et al. 2002; Marcarelli et al. 2006; Segal et al. 2006; Demetriou et al. 2007; Allakhverdiev and Murata 2008; Melgar et al. 2008; Pandey and Yeo 2008; Pandey et al. 2009; Bybordi et al. 2010a, b, c), effects of toxic pollutants on aquatic microorganisms (Berden-Zrimec et al. 2007; Mayer et al. 1997; Halling-Sørensen et al. 2000; Katsumata et al. 2005, 2006 Kvíderová and Henley 2005; Zrimec et al. 2005; Pan et al. 2009; Yates and Rogers 2011), effect of size-fractionated phytoplankton (Malone 1980; Chisholm 1992; Li 1994; Tarran et al. 2001; Hansen and Hjorth 2002; Stibor and Sommer 2003; Tittel et al. 2003; Cermeno et al. 2005; Unrein et al. 2007; Zubkov et al. 2007; Zubkov and Tarran 2008), and effects of global warming (Mostofa et al. 2009; Baulch et al. 2005; Yates and Rogers 2011; Morris and Hargreaves 1997; Cooke et al. 2006; Huisman et al. 2006; Llewellyn 2006; Richardson 2007; Malkin et al. 2008; Prince et al. 2008; Davis et al. 2009; Castle and Rodgers 2009; Mostofa and Sakugawa 2009; Etheridge 2010; Keeling et al. 2010). These factors have been assessed in recent studies and are vital to understanding and solving the debate about the occurrence of photosynthesis in terrestrial plants and aquatic microorganisms.

This chapter will give a general overview on photosynthesis, its key biogeochemical functions, the functions of photosystems (I and II) in organisms during photosynthesis, and will describe a new hypothesis for photosynthesis that adopts H_2O_2 instead of H_2O. It will also address the debates/questions regarding O_2 release from PSI and PSII during photosynthesis. Finally, it will extensively discuss the key factors that may significantly influence the photosynthetic activities of organisms, including higher plants.

2 Photosynthesis in Natural Waters

Photosynthesis is typically defined as a combination of photoinduced and biological processes that can convert carbon dioxide (CO_2) and hydrogen peroxide (H_2O_2: photoinduced generation from dissolved oxygen in water) into organic compounds (e.g. carbohydrates) and O_2 using the sunlight energy. These processes take place in photosynthetic cells of higher plants, cyanobacteria (or algae) and bacteria. Carbohydrates are then used for metabolic activities within the cell, and the whole process is termed as the oxygenic photosynthesis. It should be noted that cyanobacteria are not bacterial but generally referred to as algae. The chloroplast pigments of all cyanobacteria and aquatic higher plants have absorption bands in the blue region of the spectrum, such as the chlorophyll Soret band, and carotenoid bands (Kirk 1976). The action spectrum of photosynthesis in green algae, brown algae, diatoms and euglenas has two broad and intense peaks in the range from 400 to 500 nm of wavelength and in the region from 670 to 700 nm, respectively (Kirk 1976; Haxo and Blinks 1950; Mann and Myers 1968; Kirk and Reade 1970; Iverson and Curl 1973; Telfer et al. 1990; Schelvis et al. 1992; Durrant et al. 1995; Renger and Marcus 2002; Zhang et al. 2009). Photons of light initiate photosynthesis through releases of electrons across a membrane. It is catalysed by a special type of membrane-bound pigment-protein complexes called photosynthetic reaction centers (RCs). They are composed of photosystem I (PSI) and photosystem II (PSII), which will be discussed in the next sections. Oxygenic photosynthesis is caused by cooperation of PSI and PSII RCs and generally occurs in higher plants, bacteria and cyanobacteria. Cyanobacteria, in contrast to higher plants, are well enriched with PSI as compared with PSII: the PSI/PSII ratio is about unity in higher plants, but it is much higher in cyanobacteria, varying between 3 and 5.5 (Rakhimberdieva et al. 2001). On the other hand, either PSI or PSII RCs are used to convert light energy in anoxygenic photosynthesis, which typically occurs in many bacteria. Anoxygenicphotosynthesis is a process where uptake of light energy occurs without the release of O_2. Anoxygenic species can utilize hydrogen sulfide (H_2S) or other species as sources of reductants, giving various forms of sulfur as by-products. It is noted that green bacteria can use H_2S, while purple sulfur bacteria (*Thiorhodaceae*) can use various reduced sulfur compounds including $Na_2S_2O_3$, Na_2SO_3, S and H_2S, molecular hydrogen (H_2) and organic substances during photosynthesis (van Niel 1931; 1936; Roelofsen 1935; Muller 1933). Anoxygenic species are mostly equipped with variety of bacteriochlorophylls.

The chlorophyll absorption bands at the red end of the spectrum are only of limited use in water ecosystems, because of the rapid attenuation of red light by water (Kirk 1976). Therefore, the ability of many cyanobacteria and aquatic higher plants to photosynthesize and grow are markedly affected by the availability of blue light, which is in turn highly dependent on the concentration of yellow substance within water (Kirk 1976). All natural waters generally contain a significant amount of yellow substances that absorb light in the blue and ultraviolet (Hutchinson 1957; Kalle 1966; Jerlov 1968; Morel et al. 2007). Yellow substances originate generally from the occurrences of both allochthonous humic substances (fulvic and humic acids) of terrestrial plant origin and autochthonous fulvic acids of algal or phytoplankton origin, which absorb light in the blue and ultraviolet range (see also chapters "Dissolved Organic Matter in Natural Waters" and "Fluorescent Dissolved Organic Matter in Natural Waters") (Mostofa et al. 2009; Mostofa et al. 2009; Zhang et al. 2009; Hutchinson 1957; Kalle 1966; Jerlov 1968; Parlanti et al. 2000).

2.1 *Biogeochemical Functions of Photosynthesis*

The different functions of photosynthesis can be summarized as follows: (i) Photosynthetic oxygen production by cyanobacteria can lead to oxygenation of the atmosphere and oceans, in turn allowing aerobic respiration and the evolution of large, complex and ultimately intelligent organisms (Catling et al. 2005). Oxygenic photosynthesis has evolved hundreds of millions of years before the atmosphere became permanently oxygenated. Therefore, biogenic oxygen production started very early in Earth's history, before the start of the geological record, leading to an Archaean (greater than 2.5 Ga, gigaannum: 10^9 years) atmosphere that was highly oxygenated (Ohmoto 1997; Catling and Claire 2005; Buick 2008). (ii) Photosynthesis is the only process that can balance the biosphere by converting atmospheric CO_2 into organic/biological matter, at the same time by releasing O_2 into the atmosphere. (iii) All forms of life in the biosphere are dependent on food and primarily on vegetables and terrestrial plants, the matter of which is produced through photosynthesis. (iv) Plant litter materials or biomass, developed initially through photosynthesis, represent the largest pool of terrestrial carbon. It is currently estimated at approximately 1500–2000 Pg of C that are stored in the world's soils (Schlesinger 1997; CAST 2004). Upon microbial processing, this material can produce soil organic matter or allochthonous dissolved organic matter (DOM), including humic substances (fulvic and humic acids) and inorganic components such as nutrients and various elements (see also chapter "Dissolved Organic Matter in Natural Waters") (Mostofa et al. 2009; Nakane et al. 1997; Uchida et al. 2000; Kögel-Knabner 2002; Grandy and Neff 2008; Moore et al. 2008; Braakhekke et al. 2011; Spence et al. 2011; Tu et al. 2011). These chemical components are ultimately released into the water ecosystem and undergo photoinduced and microbial degradation. Their end-products are CO_2, H_2O_2 and dissolved inorganic carbon (DIC: generally defined as dissolved CO_2, H_2CO_3, HCO_3^-, and CO_3^{2-}), which can fuel/accelerate the primary production (see also chapter "Photoinduced and Microbial Degradation of Dissolved Organic Matter in Natural Waters" and "Impacts of Global Warming on Biogeochemical Cycles in Natural Waters") (Mostofa et al. 2009; Jones 1992; Hessen and Tranvik 1998; Jansson et al. 2000; Meili et al. 2000; Grey et al. 2001; Hernes and Benner 2003; Tranvik et al. 2009; Ballaré et al. 2011; Zepp et al. 2011). (v) Photosynthesis is the key process for primary and secondary production and uses natural sunlight in aquatic ecosystems. Aquatic microorganisms that are key components of the Earth's biosphere can produce more than 50 % of the biomass of our planet through photosynthesis, using allochthonous DOM and nutrients. Therefore, aquatic environments can incorporate at least the same amount of atmospheric carbon dioxide (CO_2) as terrestrial ecosystems (de Haan 1974, 1977; Tranvik 1988; Häder et al. 2003; Zepp et al. 2007). Life is mostly composed of the elements carbon, hydrogen, nitrogen, oxygen, sulfur and phosphorus, which make up nucleic acids (e.g. DNA), proteins and lipids and can thus form the bulk of living matter (Wolfe-Simon et al. 2011). (vi) Aquatic microorganisms (e.g. algae or phytoplankton cells) can produce autochthonous DOM, including autochthonous fulvic acids, CO_2 and nutrients under both photoinduced and microbial respiration or assimilation (see also chapters "Dissolved Organic Matter in Natural Waters", "Photoinduced and Microbial Degradation of Dissolved Organic Matter in Natural Waters", "Fluorescent Dissolved Organic Matter in Natural Waters", and "Impacts of Global Warming on Biogeochemical Cycles in Natural Waters") (Mostofa et al. 2009; Mostofa et al. 2009; Zhang et al. 2009; Tranvik et al. 2009; Biddanda and Benner 1997; Gobler et al. 1997; Kritzberg et al. 2006; Mostofa et al. 2011). These compounds can be used by aquatic microorganisms for their further photosynthetic activity and can, therefore, promote the primary production (see also chapters "Dissolved Organic Matter in Natural Waters", and "Impacts of Global Warming on Biogeochemical Cycles in Natural Waters") (Hessen and Tranvik 1998; Cole et al. 1982). (vii) Photosynthesis is the dominant energy mobilization process for secondary production in natural waters, where organic carbon fixed by primary producers is consumed directly by grazing or is recycled via the microbial loop (Wetzel 2001). (viii) The primary producers in freshwater and marine ecosystems can constitute the basis of the intricate food webs, providing energy for the primary and secondary consumers. Therefore, they are important contributors for the production of the human staple diet in the form of crustaceans, fish, and mammals derived from the sea (Häder et al. 2007). (xi) Cyanobacteria (e.g., mostly *Anabaena* and *Nostoc* spp.) that grow through photosynthesis are a rich source of potentially useful marine natural products (secondary metabolites) that have specific activities such as anti-HIV, anticancer, antifungal, antimalarial, antifoulants, anti-inflammatory, antituberculosis, and antimicrobial (Moore 1996; Burja et al. 2001; Singh et al. 2002; Blunt et al. 2007). For example cyanovirin (CV-N, cyanovirin-N), a 101 amino acid protein extracted from *Nostoc ellipsosporum* has potent activity against a wide range of immunodeficiency viruses such as HIV-1, M-and T-tropic stains of HIV-1, HIV-2, SIV (simian) and FIV (feline) (Burja et al. 2001). (x) Marine microorganisms could be used as sources of natural bioactive molecules that play a photoprotective role, which could be used in commercial applications (Rastogi et al. 2010). A number of photoprotective compounds such as melanins, mycosporines, mycosporine-like amino acids (MAAs), scytonemin, parietin, usnic acid, carotenoids, phycobiliproteins, phenylpropanoids and flavonoids and several other UV-absorbing substances of unknown chemical structure are produced by different microorganisms (Rastogi et al. 2010; Blunt et al. 2007; Jeffrey et al. 1999; Gauslaa and McEvoy 2005; Sinha et al. 2007b; Coesel et al. 2008; Klisch and Häder 2008; Hylander et al. 2009; Lee and Shiu 2009; Ingalls et al. 2010).

3 New Hypothesis for Photosynthesis Using H_2O_2 Instead of H_2O

Studies demonstrate that the reaction of CO_2 and H_2O_2 (instead of H_2O) can cause photosynthesis of organisms in photosynthetic cell in new hypothesis (Komissarov 1994, 1995, 2003; Velthuys and Kok 1978; Mano et al. 1987; Renger 1987; Anan'ev and Klimov 1988; Bader and Schmid 1988, 1989; Schroeder 1989; Schröder and Åkerlund 1990; Miyake and Asada 1992; Bader 1994; Mostofa et al. 2009; Kuznetsov et al. 2010; Bernardini et al. 2011; Mostofa et al. 2009). According to these studies, the reaction of CO_2 and H_2O_2 (instead of H_2O) can cause photosynthesis of organisms by either simultaneous photoinduced formation of H_2O_2 in chlorophylls bound in photosynthetic cell or photoinduced and microbial formation of H_2O_2 and CO_2 from dissolved organic matter (DOM) and particulate organic matter (POM) in aqueous media.

The general photosynthetic reaction can be expressed as follows (Eqs. 3.1, 3.2):

$$xCO_{2(H_2O)} + yH_2O_{2(H_2O)} \xrightarrow{h\nu} C_x(H_2O)_y + O_2 + E(\pm) \tag{3.1}$$

$$2H_2O_2 + \text{ photoinduced/biological processes } \rightarrow O_2 + 2H_2O/\text{unknown oxidants} \tag{3.2}$$

Carbohydrate $C_x(H_2O)_y$ is formed (Eq. 3.1), where x and y are whole numbers that differ depending on the specific carbohydrate that is being produced. The release of O_2 in photosynthesis is the fundamental photoinduced conversion reaction, which under the present hypothesis is supposed to involve H_2O_2 either via disproportionation or upon biological processes (Eq. 3.2) (Komissarov 2003; Buick 2008; Moffett and Zafiriou 1990; Liang et al. 2006).

The release of O_2 from H_2O_2 instead of H_2O can be understood from several mechanistic approaches: (i) Mechanism for oxygen release from H_2O_2 instead of H_2O; (ii) Effective oxidation of H_2O_2 instead of H_2O in releasing photosynthetic O_2 (iii) generation of H_2O_2 from DOM and POM; (iv) photoinduced generation of H_2O_2 from ultrapure H_2O; (v) Endogenous H_2O_2 in the photosynthetic cell and effects of exogenous H_2O_2; (vi) H_2O_2 formation in water, lipid and protein environments in the presence of Chlorophyll; and (vii) Occurrence of H_2O_2 and its effects on photosynthesis.

3.1 Mechanism for Oxygen Release from H_2O_2 Instead of H_2O

Experimental studies show that various cyanobacteria may release O_2 from the decomposition of H_2O_2 during photosynthesis (Komissarov 1994, 1995, 2003; Velthuys and Kok 1978; Mano et al. 1987; Renger 1987; Anan'ev and Klimov 1988; Bader and Schmid 1988, 1989; Schroeder 1989; Schröder and Åkerlund 1990; Miyake and Asada 1992; Bader 1994). Based on the mechanism given by Komissarov (1994, 1995, 2003) and the mechanism of H_2O_2 photodecomposition by earlier studies (Christensen et al. 1982; Bielski et al. 1985), the release of O_2 from H_2O_2 can be generalized as follows (Eqs. 3.3–3.6 or 3.7–3.10):

$$H_2O_2 \rightarrow H^+ + HO_2{}^- \tag{3.3}$$

$$HO_2{}^- + h \rightarrow HO_2 \tag{3.4}$$

$$HO_2 \rightarrow H^+ + O_2{}^- \tag{3.5}$$

$$O_2{}^- + h \rightarrow O_2 \tag{3.6}$$

or

$$H_2O_2 + HO^\bullet \rightarrow HO_2{}^\bullet + H_2O \quad k = 3.0 \times 10^7\,M^{-1}s^{-1} \tag{3.7}$$

$$HO_2{}^\bullet + HO_2{}^\bullet \rightarrow H_2O_2 + O_2 \quad k = 8.3 \times 10^5\,M^{-1}s^{-1} \tag{3.8}$$

$$HO_2{}^\bullet + O_2{}^{\bullet -} \rightarrow HO_2{}^- + O_2 \quad k = 9.7 \times 10^7\,M^{-1}s^{-1} \tag{3.9}$$

$$HO_2{}^\bullet \leftrightarrow O_2{}^{\bullet -} + H^+ \quad k = 1.58 \times 10^{-5}\,M^{-1}s^{-1} \tag{3.10}$$

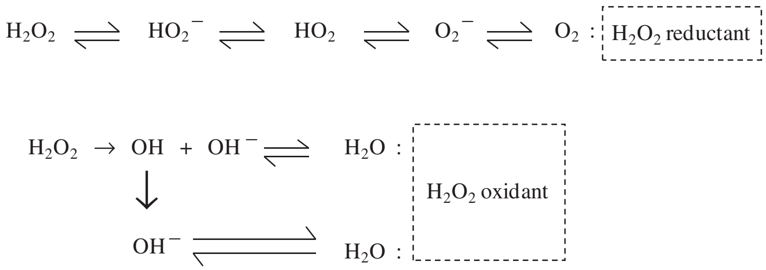


Fig. 1 Electron transfer and proton transfer reactions in the reduction of O_2 from H_2O_2 to H_2O, demonstrating the intermediates involved. *Data source* Moffett and Zafiriou (1990)

where *h* is an electron vacancy (hole), generated in the pigment under the effect of light. The generation of a single molecule of oxygen from water requires at least four light quanta, each of which generates an 'electron–hole' couple. The electron is used in the reaction ($H^+ + e \rightarrow H$) required for the subsequent fixation of CO_2.

Hylakoid particle preparations of the filamentous cyanobacterium *Oscillatoria chalybea* in laboratory experiments using labeled $^{16}O_2$ and $^{18}O_2$ show the occurrence of at least three types of oxygen uptake: one is associated with PSII and the S-state system, whereas the other two types apparently belong to the respiratory pathway. The S-state system is involved in $^{18}O_2$ production from H_2O_2 (Bader and Schmid 1988, 1989). Comparison of the relaxation kinetics of the first two flashes of a sequence with the steady-state signals as well as the detailed analysis of the mass spectrometric signals reveal that O_2 is evolved by various cyanobacteria through the decomposition of H_2O_2, which requires only two light quanta (Bader 1994).

The release of O_2 from H_2O_2 is confirmed by the redox behavior of H_2O_2 in water (Moffett and Zafiriou 1990; Rose and Waite 2003; Jeong and Yoon 2005). When H_2O_2 acts as a reductant, O from H_2O_2 is transformed into O_2 (Moffett and Zafiriou 1990). When H_2O_2 acts as an oxidant, O from H_2O_2 is converted into H_2O (Moffett and Zafiriou 1990). The chain reactions of H_2O_2 as reductant and oxidant are schematically depicted below (Fig. 1) (Moffett and Zafiriou 1990):

The detailed mechanism for the release of O_2 in the first scheme can be generalized using the reduction of Fe^{3+} (or Cu^{2+}) by H_2O_2 in the following ways (Eqs. 3.11–3.15) (Bielski et al. 1985; Hardwick 1957; Moffett and Zika 1987a, b; Marianne and Sulzberger 1999):

$$HOOH \leftrightarrow H^+ + HO_2^- \tag{3.11}$$

$$Fe^{3+} + HO_2^- \rightarrow Fe^{2+} + HO_2^{\bullet} \tag{3.12}$$

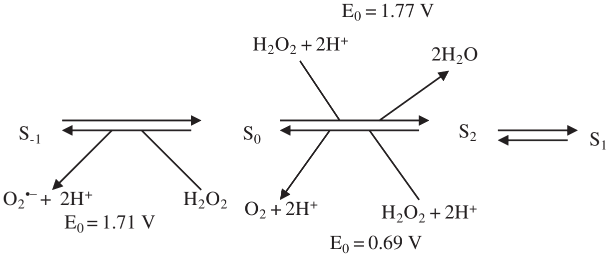
$$HO_2^{\bullet} \leftrightarrow H^+ + O_2^{\bullet -} \quad k = 1.58 \times 10^{-5}\,M^{-1}s^{-1} \tag{3.13}$$

$$Fe^{3+} + O_2^{\bullet -} \rightarrow Fe^{2+} + O_2 \quad k = 1.5 \times 10^{8}\,M^{-1}s^{-1} \tag{3.14}$$

$$H_2O_2 + Fe^{2+} \rightarrow Fe^{3+} + HO^{\bullet} + OH^- \quad k = 63\,M^{-1}s^{-1} \tag{3.15}$$

In the reactions above, release of O_2 occurs not from H_2O but from H_2O_2.

Correspondingly, photosynthetic O_2 evolution would involve different stages that carry out a gradual accumulation of oxidizing equivalents in the Mn-containing water-oxidizing complex (WOC) (Samuilov et al. 2001). The WOC can exist in different oxidation states (S_n, where high n indicates the most oxidised states), which can be probed by addition of different redox-active molecules. The interaction of H_2O_2 with the S states of the WOC is depicted in the scheme that follows (Velthuys and Kok 1978; Mano et al. 1987; Samuilov et al. 2001; Latimer 1952; Ilan et al. 1976; Samuilov 1997):



These studies suggest that H_2O_2 is an evolutionary precursor of H_2O as the electron donor for PSII in cyanobacteria (Bader 1994; Samuilov 1997; Blankenship and Hartman 1998).

The release of O_2 from H_2O_2 instead of H_2O can be justified by the rapid formation of H_2O_2 and of highly reactive chemical forms collectively denoted as 'reactive oxygen species (ROS)'. Both H_2O_2 and ROS are formed from O_2 when it is exposed to high-energy or electron-transfer chemical reactions, which can be expressed as follows (Chance et al. 1979; Koppenol 1976; Klotz 2002; Apel and Hirt 2004):

$$3O_2 + h\upsilon \rightarrow {}^1O_2 \rightarrow {}^1O_2 \tag{3.16}$$

$$3O_2 + e^- + h\upsilon \rightarrow O_2{}^{\bullet-} \xrightarrow{H+} HO_2{}^{\bullet} \tag{3.17}$$

$$O_2{}^{\bullet-} + e^- + h\upsilon \rightarrow O_2{}^{2-} \xrightarrow{2H+} H_2O_2 \tag{3.18}$$

$$O_2{}^{2-} + e^- + h\upsilon \rightarrow O_2{}^{3-} \begin{array}{l} \rightarrow O^- \overset{H^+}{\rightarrow} HO^{\bullet} \\ \downarrow 2H^+ \\ H_2O \end{array} \tag{3.19}$$

$$O^- + e^- + h\upsilon \rightarrow O^{2-} \xrightarrow{2H+} H_2O \tag{3.20}$$

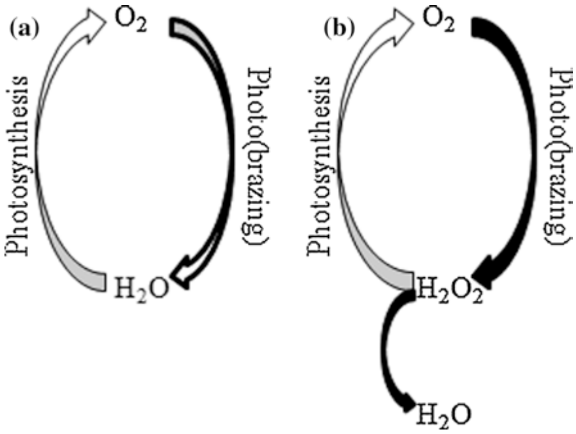


Fig. 2 The relationship between photosynthesis and (photo) bleeding within the framework of the conventional considerations regarding photosynthesis (**a**) and in accordance with the concept proposed by the author of the article (**b**). *Data source* Komissarov (2003)

Singlet oxygen ($^1O_2$) and superoxide radical ion $\left(O_2{}^{\bullet-}\right)$ are formed from the triplet state of O_2 $\left(^3O_2\right)$ in the presence of light (Eqs. 3.16, 3.17). The radical ion $O_2{}^{\bullet-}$ then reacts with an hydrogen ion (H^+) to form the perhydroxyl radical $(HO_2{}^{\bullet})$ (Eq. 3.17). The species $O_2{}^{\bullet-}$ can also accept one more electron (e^-) to form peroxide ion ($O_2{}^{2-}$), which then combines with H^+ to generate hydrogen peroxide (H_2O_2) (Eq. 3.18). Further acceptance of one e^- by $O_2{}^{2-}$ can form $O_2{}^{3-}$, which can then produce H_2O and an oxene ion (O^-) in the presence of H^+ (Eq. 3.19). The ion radical O^- can produce the hydroxyl radical in the presence of H^+ (Eq. 3.19). Further acceptance of one e^- by O^- can yield the oxide ion (O^{2-}), which finally gives H_2O in the presence of H^+ (Eq. 3.20). This result shows that formation of water from O_2 is relatively more difficult than the process involving H_2O_2.

In the new hypothesis, the relationship between the fundamental biological process and breathing is complicated because the final product in breathing is water, which would not dissociate during photosynthesis (Fig. 2b) (Komissarov 2003). This is not contemplated in the conventional view of photosynthesis, which is illustrated in Fig. 2a. Breathing is followed from right to left in both equations.

However, breathing is accompanied by the formation of endogenous H_2O_2 that is not only a source of O_2, injected into the atmosphere, but also of hydrogen used in the synthetic processes of growth (Komissarov 2003).

Mass spectrometric examination of photosynthetic generation of O_2 using H_2O_2, marked with heavy isotopic oxygen $\left(H_2{}^{18}O_2\right)$, suggests that H_2O_2 is the source of the entire amount of generated O_2 (Mano et al. 1987). Experimental studies using ^{18}O-labeled H_2O_2 $\left(H_2{}^{18}O_2\right)$ and O_2 $\left(^{18}O_2\right)$ added to seawater also suggest that photoinduced oxidation can produce $^{18}O_2$and H_2O (Moffett and Zafiriou 1990), whereas label transfer is governed by the mass balance (Eq. 3.21):

$$-\Delta H_2{}^{18}O_2 = \Delta H_2{}^{18}O + \Delta{}^{18}O_2 \tag{3.21}$$

Similarly, catalytic epoxidation experiments using the ^{18}O labels in an acetone/water $\left(H_2{}^{18}O\right)$ solvent demonstrate that no ^{18}O coming from water $\left(H_2{}^{18}O\right)$

is incorporated into epoxide products, even though oxygen exchange is observed between the Mn^{IV} catalyst species and $H_2{}^{18}O$. Therefore, one can conclude that O_2 transfer does not proceed by the well-known oxygen-rebound mechanism (Yin et al. 2006). Experiments using labeled dioxygen, $^{18}O_2$, and hydrogen peroxide, $H_2{}^{18}O_2$, confirm that an oxygen atom is transferred directly from the $H_2{}^{18}O_2$ oxidant to the olefin substrate in the predominant pathway (Yin et al. 2006). Moreover, some recent experiments show that photoinduced H_2O oxidation occurs in the presence of inorganic catalysts (Kuznetsov et al. 2010; Bernardini et al. 2011). This result does not imply that H_2O is oxidized, but rather that $O_2{}^{\bullet -}$ and then H_2O_2 are produced photolytically. H_2O_2 is then photolytically decomposed into O_2 and H_2O.

Biological release of O_2 is observed using catalase for the decomposition of H_2O_2 in aqueous media, a process that can be depicted as follows (Eqs. 3.22, 3.23) (Moffett and Zafiriou 1990):

$$\mathrm{HOOH} + \mathrm{Catalase} \rightarrow \mathrm{HOOH}^{*} + \mathrm{Catalase}^{\#} \tag{3.22}$$

$$2\mathrm{HOOH}^{*} + \mathrm{Catalase}^{\#} \rightarrow \mathrm{H{-}O{-}H} + O_2 + \mathrm{Catalase} \tag{3.23}$$

In the above reactions, catalase enzymatically activates HOOH^{*} to use them as oxidants (electron acceptors) and reductants (electron donors) (Eq. 3.22). Afterwards, disproportionation of activated HOOH^{*} converts them into H_2O and O_2 (Eq. 3.23). Therefore, H_2O_2 can release O_2 under both photoinduced and microbial decomposition processes. The widespread occurrence of such a process justifies the hypothesis that the release of photosynthetic O_2 may occur from H_2O_2 instead of H_2O. Note that the contribution percentage decay of H_2O_2 is 65–80 % by catalase enzyme and 20–35 % by peroxidase enzyme, as estimated by isotopic measurements in seawater (Moffett and Zafiriou 1990).

Based on the current evidence, it is hypothesized that oxygenic photosynthesis has evolved by the end of the 'Great Oxidation Event' *ca.* 2.4 Ga ago. It has permanently raised atmospheric oxygen above the levels produced by photolysis of water (Buick 2008). The latter process can produce primarily H_2O_2, which might be source of oxygenic photosynthesis.

3.2 *Effective Oxidation of H_2O_2 Instead of H_2O in Releasing Photosynthetic O_2*

The oxidation of water to molecular oxygen is described by the equation (Rappaport and Diner 2008): $2H_2O \rightarrow O_2 + 4H^+ + 4e^-$, where at pH 7.0 the midpoint potential of the $O_2/2H_2O$ couple is 810 mV. Water is a very stable molecule and its oxidation requires the successive absorption of four photons and their photoinduced conversion into electrochemical energy. The energy of the quantum of a visible light is relatively small, such as 1.8 eV at the maximum absorption of chlorophyll (Komissarov 2003).

The value of standard electrode potential of the reaction of O_2 formation from H_2O_2 (Eq. 3.19) is significantly lower than for H_2O (Eqs. 3.24, 3.25) (Komissarov 2003):

$$H_2O_2 = O_2 + 2H^+ + 2e^-, \quad E^0 = -0.69\ \mathrm{V} \tag{3.24}$$

$$H_2O = 1/2O_2 + 2H^+ + 2e^-, E^0 = -1.23\ \mathrm{V} \tag{3.25}$$

Therefore, in vivo formation of oxygen would be preferable from hydrogen peroxide than from water.

3.3 Generation of H_2O_2 from DOM and POM

The most important source of H_2O_2 is the photoinduced generation from DOM and POM (e.g. algae) under solar illumination in natural waters. The mechanism has been discussed in earlier chapters (see "Photoinduced and Microbial Generation of Hydrogen Peroxide and Organic Peroxides in Natural Waters" and "Chlorophylls and Their Degradation in Nature"). In addition, DOM can also produce H_2O_2 under dark incubation. Algae or phytoplankton can produce H_2O_2 from superoxide radical anion $(O_2^{\bullet-})$, which can be formed either by photoinduced generation of electrons from Chlorophyll bound in microorganisms, or via autochthonous DOM. In the latter case, H_2O_2 generation can take place under photo- and microbial respiration (assimilations) of phytoplankton (see chapter "Photoinduced and Microbial Generation of Hydrogen Peroxide and Organic Peroxides in Natural Waters" and "Chlorophylls and Their Degradation in Nature"). Overall, production of H_2O_2 from various sources can be depicted as follows (Fig. 3).

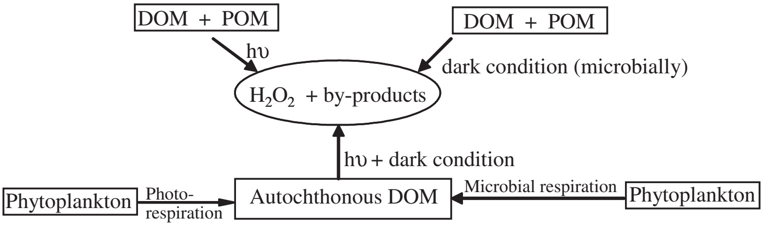


Fig. 3 Production of H_2O_2 from various sources in natural waters

3.4 Endogenous H_2O_2 in the Photosynthetic Cell and Effects of Exogenous H_2O_2

Endogenous H_2O_2 is formed in photosynthetic cells of organisms through production of superoxide radical ion $(O_2^{\bullet-})$ from whole bacteria of several species, from phagocytic cells, from spermatozoa as well as peroxisomes, mitochondria and chloroplasts (Komissarov 2003; Bach 1894; Chance et al. 1979; Halliwell 1981; Holland et al. 1982; Wilhelm et al. 1996, 1997, 1999; Halliwell and Gutteridge 1999; López-Huertas et al. 1999; Baker and Graham 2002; del Río et al. 2006; Krieger-Liszkay et al. 2008; Lyubimov and Zastrizhnaya 1992a, b; Turrens 1997; Karuppanapandian et al. 2011). H_2O_2 is also detected in the lens of the human eye and cataracts, aqueous humor and urine, in expired human breath and rat breath. Furthermore, increased H_2O_2 concentrations are also observed in patients with the adult respiratory distress syndrome, in patients with a cardiopulmonary bypass, in people exposed to ozone, in alveolar and peritoneal macrophages isolated from rats exposed to hypoxia, and in the breath of smokers (Wilhelm et al. 1996, 1997; Bhuyan and Bhuyan 1977; Spector and Garner 1981; Williams and Chance 1983; Ramachandran et al. 1991; Wilson et al. 1993; Nowak et al. 1996; Madden et al. 1997).

It has also been observed that oral bacteria may produce H_2O_2 (Thomas and Pera 1983) and that several enzymes, including glycollate and urate oxidases, can produce H_2O_2. It is calculated that 82 nM of H_2O_2 is produced per g of tissue per min in perfused livers isolated from normally fed rats (Chance et al. 1979). The H_2O_2 production rate is increased with inclusion of glycollate or urate in the perfusion medium. H_2O_2 is a precursor of $HO^\bullet$, a strong oxidizing agent, which is mostly formed either in the Fenton-type reaction in the presence of transition metals or via the Haber–Weiss reaction in the presence of superoxide and iron (Fong et al. 1976). Catalase, the enzyme that metabolizes H_2O_2 to H_2O and O_2 is detected in liver, kidney, blood, mucous membranes and other highly vascularized tissues (Sohal et al. 1994; Matutte et al. 2000). Correspondingly, detoxification of H_2O_2 by catalase has also been observed in the rabbit iris-ciliary body and in cultured lens epithelial cells (Delamere and Williams 1985; Giblin et al. 1990).

The radical ${O_2}^{\bullet -}$ can rapidly produce H_2O_2 and O_2 by the following reaction (Eq. 3.26) (Koppenol 1976):

$$2{O_2}^{\bullet -} + 2H^+ \rightarrow H_2O_2 + O_2 \quad k = 4.5 \times 10^5 M^{-1} s^{-1} \text{at pH 7 and } 22^\circ C \tag{3.26}$$

although the reaction between ${O_2}^{\bullet -}$ and ${HO_2}^\bullet$ is much faster.
Similarly, $HO^\bullet$ can react with ${O_2}^-$ to produce H_2O and O_2 (Eq. 3.27) (Koppenol 1976):

$$HO^\bullet + {O_2}^- + H^+ \rightarrow O_2 + H_2O \tag{3.27}$$

Several studies have proposed that $^1O_2$ is formed in the cells or in PSII (Halliwell and Gutteridge 1999; Krieger-Liszkay et al. 2008; Kautsky et al. 1931; Durrant et al. 1990; Vass et al. 1992; Macpherson et al. 1993; Hideg et al. 1994; Keren et al. 1997; Fufezan et al. 2002; Krieger-Liszkay 2005). The chlorophyll (Chl) triplet state can produce the very reactive $^1O_2$ upon reaction with ground state $^3O_2$, if it is not efficiently quenched (Krieger-Liszkay et al. 2008). The lifetime of $^1O_2$ in a cell is estimated into approximately 3 s (Skovsen et al. 2005; Hatz et al. 2007).

The reactive transient $^1O_2$ is also formed from superoxide anion (O_2^-) in the following process (3.28) (Koppenol 1976):

$$O_2^- \rightarrow {}^1O_2 + e^- \text{ where } E_0 = +0.65\ \text{V} \tag{3.28}$$

In addition, any sensitizer (e.g. photoactive organic matter) can photolytically produce $^1O_2$ via the following processes (Eqs. 3.29, 3.30) (Braun and Oliveros 1990):

$$\text{Sens} + h\upsilon \rightarrow {}^1\text{Sens}^* \rightarrow {}^3\text{Sens}^* \tag{3.29}$$

$$^3\text{Sens}^* + O_2 \rightarrow \text{Sens} + {}^1O_2 \tag{3.30}$$

where Sens is the sensitizer that can absorb photons and is promoted to the singlet excited state $\left({}^1\text{Sens}^*\right)$. The latter can undergo intersystem crossing (ISC) and be converted into the triplet state $\left({}^3\text{Sens}^*\right)$ (Eq. 3.29), which can react with O_2 to produce $^1O_2$ (Eq. 3.30).

On the other hand, deactivation of $^1O_2$ involves two major processes such as energy-transfer quenching and charge-ransfer quenching,through any acceptor or sensitizer (Eqs. 3.31, 3.32) (Braun and Oliveros 1990; Halliwell and Gutteridge 2007):

$$^1O_2 + \text{Sens} \rightarrow \text{SensO}_2 \tag{3.31}$$

$$\text{SensO}_2 \rightarrow O_2 + \text{Sens} \tag{3.32}$$

The H_2O_2 concentration in plant cells is approximately 0.5–1 μmol per milligram of Chl, including Chl of photosynthetic antennae (Lyubimov and Zastrizhnaya 1992a). Therefore, the amount of H_2O_2 is much higher than the Chl content in the composition of so called oxygen-evolving complexes in chloroplasts (Lobanov et al. 2008). Experimental studies have shown that the content of H_2O_2 can increase during ontogenesis of both the whole plant and populations of protoplasts of separate leaves in the dark, and the light-dependent component of peroxide formation increases regardless of the metabolic type of the plant antennae (Lyubimov and Zastrizhnaya 1992b). It is known that each molecule of the chlorophyll absorbs light quanta ~1 time per second, even at the maximum intensity of daylight (Komissarov 2003). Synthetic Chl, metal complexes of porphyrins and phthalocyanines are photoactive and can produce H_2O_2 under irradiation in aqueous solutions saturated with O_2 (Lobanov et al. 2008; Hong et al. 1987; Bazanov et al. 1999; Premkumar and Ramaraj 1999).

Lower volatility of H_2O_2 compared to H_2O may cause the green leaves to be a unique concentrator of H_2O_2 (Komissarov 2003). It is shown that the heat of vapour formation of pure H_2O_2 is 12.3 kcal mole^{-1}, whilst that of water is 10.5 kcal mole^{-1} (Shamb et al. 1958). Transpiration (evaporation of water by plants) may evidently play the same function of H_2O_2 concentrator in addition to the protection of plants against overheating. For each kg of water, absorbed by the roots from soil, only 1 g is used by the plant for the construction of tissue. Therefore, the transpiration process may enhance the total contents of H_2O_2 in the plant cells. Terrestrial plants can receive high concentrations of rainwater H_2O_2 (0–199,000 nM: see Table 2 in chapter "Photoinduced and Microbial Generation of Hydrogen Peroxide and Organic Peroxides in Natural Waters"), which is a vital source of exogenous H_2O_2 and is susceptible to promote photosynthesis in plants and algae (Komissarov 1994, 1995, 2003; Mostofa et al. 2009). Experimental studies demonstrate that H_2O_2 concentrations (up to 10^{-5} M) in culture media can stimulate plant growth (Komissarov 1994, 1995, 2003). In addition, H_2O_2 can inhibit growth at concentrations as low as 10^{-5}–10^{-4} M under the conditions of a dialysis culture (Samuilov et al. 2001). H_2O_2 can inhibit the photosynthetic electron transport in cells of cyanobacteria (Samuilov et al. 2001, 2004) and can also destroy the function of the oxygen-evolving complex (OEC) in some chloroplasts and photosystem II preparations. In such a case it would cause the release of manganese from cyanobacterial cells, which inhibits the OEC activity.

3.5 H_2O_2 Formation in Water, Lipid and Protein Environments in the Presence of Chlorophyll

Chlorophyll can produce H_2O_2 in aqueous solution under acidic and alkaline pH conditions (pH = 3.8–12.4) under visible light irradiation (Lobanov et al. 2008). The mechanism behind the production of H_2O_2 from illuminated Chl can be illustrated as follows (3.33–3.39) (Lobanov et al. 2008; Parmon 1985; Bruskov2002):
At pH < 7

$$\mathrm{Chl} + h\upsilon \rightarrow \mathrm{Chl}^* \tag{3.33}$$

$$\mathrm{Chl}^* + O_2 \rightarrow \mathrm{Chl}^+ + O_2^{\bullet -} \tag{3.34}$$

$$O_2^{\bullet -} + H^+ \rightarrow HO_2^{\bullet} \quad k = 5 \times 10^{10}\,\mathrm{Ms}^{-1} \tag{3.35}$$

$$HO_2^{\bullet} + O_2^{\bullet -} + H^+ \rightarrow H_2O_2 + O_2 \quad k = 9 \times 10^{7}\,\mathrm{Ms}^{-1} \tag{3.36}$$

$$HO_2^{\bullet} + HO_2^{\bullet} \rightarrow H_2O_2 \quad k = 2 \times 10^{6}\,\mathrm{Ms}^{-1} \tag{3.37}$$

At pH > 7

$$H_2O_2 + Fe^{2+}\ (\text{or other metals}) \rightarrow HO^{\bullet} + HO^{-} + Fe^{3+} \tag{3.38}$$

$$HO^{\bullet} + HO^{\bullet} \rightarrow H_2O_2 \quad k = 6 \times 10^{9}\,\mathrm{Ms}^{-1} \tag{3.39}$$

The electron donor for the conversion $O_2 \rightarrow O_2^{\bullet -}$ (redox potential $\phi^\circ = -0.12$ V) can be Chl in the singlet or triplet excited state (the S1 and T1), with $\phi^\circ = -1.14$ and -1.54 V, respectively (Lobanov et al. 2008). The occurrence of reaction (Eq. 3.39) is confirmed by the addition of 1 M ethanol as a scavenger of $HO^{\bullet}$ into the water suspension of silica gel with immobilized Chl inhibits the formation of H_2O_2 in the alkaline medium with pH 12.4 (Lobanov et al. 2008; Bruskov and Masalimov 2002). Formation of H_2O_2 from Chl can generally be expressed as follows (Eq. 3.40) (Lobanov et al. 2008): at pH < 7,

$$1/2O_2 + H^+ + \mathrm{Chl} + h\upsilon \rightarrow 1/2H_2O_2 + \mathrm{Chl}^+ \tag{3.40}$$

where redox potentials ($\Delta\varphi°$) and Gibbs energy changes (ΔG^0) for the reduction of O_2 to H_2O_2 with simultaneous oxidation of Chl to the radical cation ($T = 298$ K) are -0.03 V and 5.8 kJ for H_2O_2 generation, 1.83 V and -353 kJ for the singlet excited state of Chl, as well as 1.23 V and -237 kJ for the triplet excited state of Chl, respectively.Similarly at pH > 7 (Eq. 3.41),

$$1/2O_2 + \mathrm{Chl} + h\upsilon \rightarrow 1/2HO_2{}^- + \mathrm{Chl}^+ \tag{3.41}$$

where $\Delta\varphi°$ and ΔG^0 for the reduction of O_2 to $HO_2{}^-$ with simultaneous oxidation of Chl to the cation radical ($T = 298$ K) are -0.80 V and 154 kJ for $HO_2{}^-$ generation, 1.06 V and -204 kJ for the singlet excited state of Chl, and 0.46 V and -89 kJ for the triplet excited state of Chl, respectively (Lobanov et al. 2008).

In addition, H_2O_2 is significantly formed photolytically in aqueous mixtures of Chl and either micelles of cetyltrimethylammonium bromide (CTAB) or macromolecules of bovine serum albumin (BSA) in a noncovalent complex. Insuch a case, Chl acts as a photocatalyst (Lobanov et al. 2008). The Chl may affect the donors of electron density, polarize chemical bonds, and stabilize reaction intermediates (similar to enzyme–substrate complexes) by the occurrence of N-, O-, and S-containing functional groups bound in proteins and lipids (Lobanov et al. 2008).

Under certain physiological conditions such as exposure to high light intensity or drought, reduction of O_2 in photosynthetic organisms can produce reactive oxygen species (ROS), such as $O_2{}^{\bullet -}$, H_2O_2 or $^1O_2$. These species can lead to the closure of the stomata and cause low CO_2 concentrations in the chloroplasts (Krieger-Liszkay et al. 2008; Asada 1992, 2006 Halliwell and Gutteridge 1990; Hideg et al. 2001, 2002; Trebst et al. 2002). It is shown that a key ROS in UV-irradiated leaves is $O_2{}^{\bullet -}$, whilst $^1O_2$ is minor (Hideg et al. 2002). Therefore, H_2O_2 may be produced in the plant cells via $O_2{}^{\bullet -}$. Under such conditions, the plastoquinone pool can be in a very highly reduced state that would allow photoinhibition, i.e. the light induced loss of PSII activity (Adir et al. 2003). The $HO^\bullet$ produced photolytically from H_2O_2 or $^1O_2$ and ROS itself can react with proteins, pigments, nucleic acids and lipids, and could also be connected to the light-induced loss of PSII activity, to the degradation of the D1 polypeptide (PSII reaction centre polypeptide) and to pigment bleaching (Krieger-Liszkay et al. 2008; Aro et al. 1993; Nishiyama et al. 2001, 2004; Vass et al. 1992; Hideg et al. 1994; Keren et al. 1997; Halliwell and Gutteridge 1990; Sopory et al. 1990; Prasil et al. 1992; Hideg et al. 1998; Okada et al. 1996; 2006; Allakhverdiev and Murata 2004; Nixon et al. 2005; Hideg et al. 2007; Aro 2007; Tyystjärvi 2008). Such reactions are often observed in water, where photoinduced generation of $HO^\bullet$ either from H_2O_2 (both upon direct photolysis by sunlight and photo-Fenton reaction) or other sources (e.g. $NO_2{}^-$and $NO_3{}^-$) can decompose the DOM components

(Draper and Crosby 1981; Zepp et al. 1992; Wang et al. 2001; White et al. 2003; Nakatani et al. 2007; Vione et al. 2006, 2009a, b).

3.6 Occurence of H_2O_2 and its Effect on Photosynthesis

In support of the involvement of H_2O_2 in the photosynthetic reaction, several H_2O_2-related phenomena have been observed in natural waters, which can be classified as follows (Mostofa et al. 2009). First, the correlation between carbon production and photolytically formed H_2O_2 concentration, suggesting a link between hydrogen peroxide and organic matter photosynthesis in lake water (Anesio et al. 2005). Second, Chl *a* production in the epilimnetic layer (5–10 m) is typically observed to increase with a decrease in total CO_2 contents (Talling 2006), suggesting that photosynthesis is highest at the epilimnetic layer (5–10 m) than in the uppermost epilimnion (0–1 m). Correspondingly, the O_2 and Chl *a* contents reach a minimum when the water temperature become highest during the summer stratification period (Talling 2006), suggesting that photoinduced degradation or assimilation of Chl *a* may be responsible for the decrease in Chl *a* at the uppermost layer. Here O_2 may be involved in the production of free radicals (H_2O_2 or $HO^\bullet$) that could inhibit photosynthesis (Mostofa and Sakugawa 2009; Moffett and Zafiriou 1990). This result is similar to earlier studies where photosynthesis was observed to be less effective in the uppermost layer (1 m) compared to the subsequent epilimnion (3 m) (Nozaki et al. 2002). A ratio of variable to maximal fluorescence (Fv/Fm) of phytoplankton productivity showed a decrease as irradiance increased during the morning and an increase as irradiance declined in the afternoon. These results may be associated with both photoprotective strategies in the antennae of PSII and photo damage of PSII reaction centers (Zhang et al. 2008). Conversely, H_2O_2 usually increases gradually starting in the morning, reaches a maximum at noon and then gradually decreases in the afternoon (Mostofa and Sakugawa 2009). It is therefore suggested that high production of H_2O_2 and subsequent photoinduced generation of $HO^\bullet$ at noon is susceptible to damage the PSII reaction centers.

Third, H_2O_2 may be concentrated by particulate organic matter or small fungi through rapid transpiration (Komissarov 1994, 1995, 2003). This hypothesis can be supported by observation of relatively low production of H_2O_2 in unfiltered samples compared to filtered ones during irradiation (Moffett and Zafiriou 1990; Cooper et al. 1988; Petasne and Zika 1997). An increase in the growth rate of plants and mycelial fungi is detected when the H_2O_2 concentration increases up to an optimum level, from 1 nM to 10 M, and the growth rate decreases when H_2O_2 approaches 1 mM (Komissarov 2003; Ivanova et al. 2005). High levels of H_2O_2 may photolytically produce $HO^\bullet$, a strong oxidizing agent, that may cause ecophysiological disorders in plants, decrease the CO_2 assimilation rate and affect stomatal conductance, fluorescence and needle life span (Kume et al. 2000; Kobayashi et al. 2002). In natural waters, $HO^\bullet$ that is produced photolytically from

H_2O_2 can degrade phytoplankton cells, thereby decreasing photosynthesis. The synergistic effect of high contents of H_2O_2 combined with elevated seawater temperature (27–31 °C) can result in a 134 % increase in respiration rates of the coral *Galaxea fascicularis*, which can surpass the effect of either H_2O_2 or high seawater temperature alone (Higuchi et al. 2009). A possible explanation is that an increase in growth of plant species with increasing H_2O_2 might enhance carbohydrate production, and therefore enhance the activity throughout the food web.

4 Functions of Photosystems (I and II) in Organisms During Photosynthesis

Photosynthesis is primarily initiated by the light-induced release of electrons across a membrane, which is catalyzed by two multisubunits, special type of membrane-bound pigment-protein complexes called photosynthetic reaction centres (RCs). They are photosystem I (PSI) and photosystem II (PSII) (Krauß 2003; Golbeck 1994; Brettel 1997; Li et al. 2006; Rappaport and Diner 2008; Müller et al. 2010; Nilsson Lill 2011; Umena et al. 2011; Renger and Holzwarth 2005; Fromme 2008; Holzwarth 2008). PSI of higher plants and algae (named PSI-200) consists of the PSI core complex and the peripheral light-harvesting complex LHCI. In cyanobacteria, it only consists of the PSI core (Schlodder et al. 2011). The PSI core complexes in cyanobacteria are organized preferentially as trimers, whereas PSI in higher plants and algae is present only as a monomer (Boekema et al. 1987, 2001; Shubin et al. 1993; Kruip et al. 1994; Jordan et al. 2001; Amunts et al. 2010).

By studying the crystal structure of cyanobacterial PSI it has been shown that it is composed of 128 cofactors including approximately 96–100 Chl molecules, two phylloquinones, three $[Fe_4S_4]$ clusters, 22 carotenoids, four lipids and a putative Ca^{2+} ion (Fig. 4) (Krauß 2003; Krauss et al. 1993; Krauß et al. 1996; Klukas et al. 1999; Jordan et al. 2001; Ben-Shem et al. 2003; Müller et al. 2010; Webber and Lubitz 2001). The PSI antenna consists of 90 Chls, of which 79 are bound to a heterodimeric core formed by subunits PsaA and PsaB, with 2 × 11 transmembrane α-helices (Krauß 2003). The cofactors in the RC of PSI form two quasi-symmetric branches (Fig. 4), diverging from a Chl *a*/Chl *a* pair (ec1A/ec1B) traditionally called P700 (Jordan et al. 2001; Müller et al. 2010). In each branch there is a pair of Chl *a* molecules (ec2A/ec3A or ec2B/ec3B) and a phylloquinone (PhQA or PhQB) and then the branches join again at the FX iron-sulfur (FeS) cluster (Müller et al. 2010). The carotenoids have a dual function in light harvesting and photoprotection. The organic cofactors of the electron transfer chain are bound to PsaA/PsaB and arranged in two branches of three Chl and one phylloquinone molecule each, related by a pseudo-C2 axis (Krauß 2003). These studies show that the PSI reaction center or primary donor P700 in PSI is composed of six chlorophyll (Chl) *a* cofactors: the P700 special pair Chls (analogous to the special pair bacteriochlorophylls in purple bacterial reaction centers), two accessory Chls

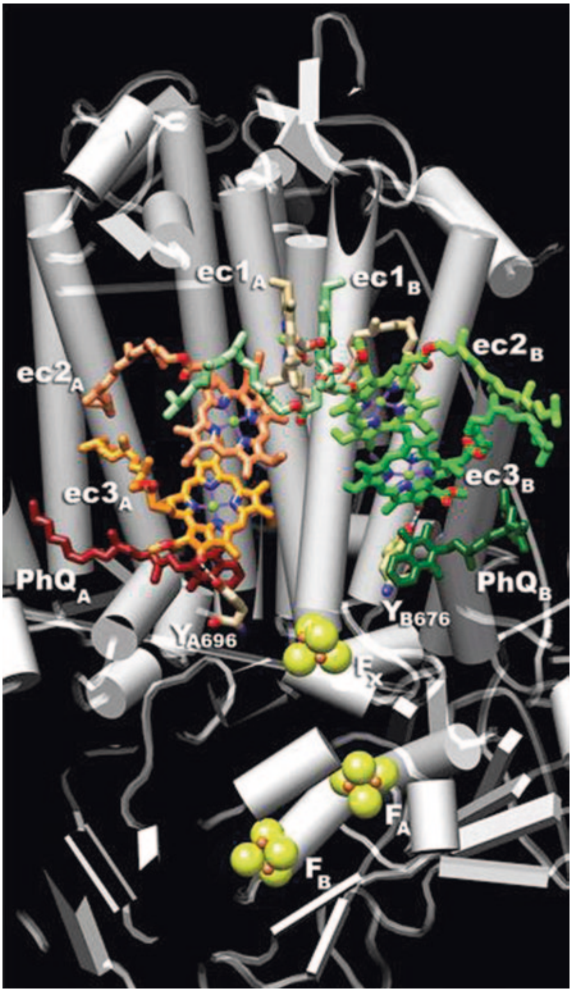


Fig. 4 Organization of the ET cofactors in the RC of PSI, based on the X-ray crystal structure of cyanobacterial PSI [1JB0] (Jordan et al. 2001), and using the nomenclature suggested by Redding and van der Est (Redding and van der Est 2006) (Figure is generated using UCSF Chimera). *Data source* Müller et al. (2010)

(analogous to the accessory bacteriochlorophylls), and two chlorophylloid. Based on the crystal structures, it is generally assumed that the PSI core complexes, particularly the cofactor arrangement in the reaction centre, are similar in all organisms and plants (Jordan et al. 2001; Ben-Shem et al. 2003).

On the other hand, crystal structure analysis of cyanobacterial photosystem II (PSII) demonstrates that PSII monomer contains 20 subunits with a total molecular mass of 350 kDa (Umena et al. 2011). It is composed of 19 protein subunits, 32–36 Chl molecules (35 Chls for *T. vulcanus*) (Umena et al. 2011) including chlorophyll *a* dimer ($P_{D1}P_{D2}$) and monomers (Chl_{D1} and Chl_{D2}), two pheophytins *a* ($Pheo_{D1}$ and $Pheo_{D2}$), 11 ß-carotenes, more than 20 lipids, two plastoquinones Q_A and Q_B, two haem irons, one non–haem iron, a tetranuclear manganese cluster forming $Mn_4CaO_5(H_2O)_4$ or $Mn_4CaO_4(OH)(H_2O)_4$, three or four calcium atoms

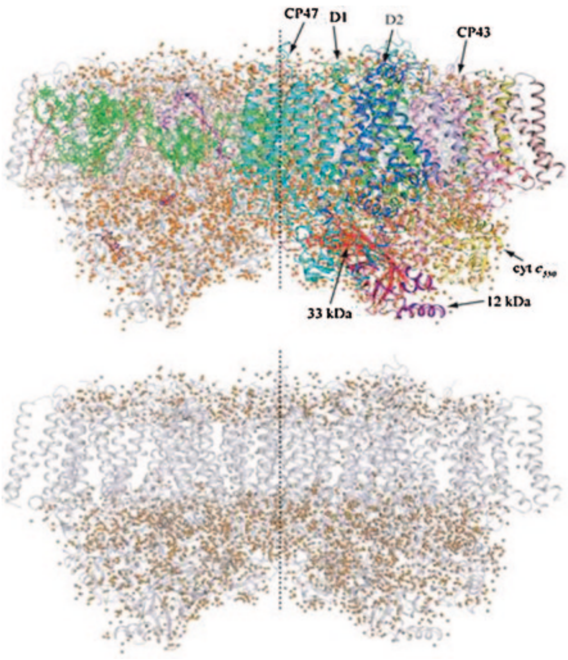


Fig. 5 Overall structure of PSII dimer from *Thermosynechococcus vulcanus* at a resolution of 1.9Å. View from the direction perpendicular to the membrane normal. **a** Overall structure. The protein subunits are coloured individually in the right hand monomer and in light *grey* in the left-hand monomer, and the cofactors are coloured in the left-hand monomer and in light *grey* in the right-hand monomer. Orange balls represent water molecules. **b** Arrangement of water molecules in the PSII dimer. The protein subunits are coloured in light *grey* and all other cofactors are omitted. The central broken lines are the noncrystallographic two-fold axes relating the two monomers. *Data source* Umena et al. (2011)

(one of which is in the Mn_4Ca cluster), three Cl^- ions (two of which are near the Mn_4CaO_5 cluster), one bicarbonate ion and more than 15 detergents (Fig. 5) (Krauß 2003; Nilsson Lill 2011; Umena et al. 2011; Zouni et al. 2001; Kamiya and Shen 2003; Ferreira et al. 2004; Loll et al. 2005; Murray et al. 2008; Kawakami et al. 2009; Guskov et al. 2009; Biesiadka et al. 2004). PSII reaction center or primary donor P680 in PSII is an approximately C_2-symmetric structure formed by polypeptides (D1 and D2) and six chlorin cofactors: four chlorophyll *a* and two pheophytin *a* ($Pheo_{D1}$ and $Pheo_{D2}$) (Fig. 5) (Nilsson Lill 2011; Umena et al. 2011). Each PSII monomer consists of more than 1,300 water molecules, yielding a total of 2,795 water molecules in the dimer (Umena et al. 2011). The water molecules are organized into two layers located on the surfaces of the stromal and lumenal sides, respectively, with the latter having more water molecules than the former (Umena et al. 2011). A few water molecules are detected within the membrane region, most of them serving as ligands to chlorophylls (Umena et al. 2011).

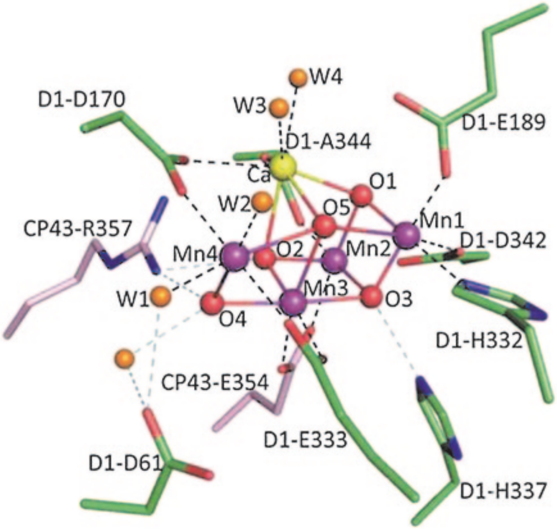


Fig. 6 Structure of the Mn_4CaO_5 cluster. Stereo view of the Mn_4CaO_5 cluster and its ligand environment. The distances shown are the average distances between the two monomers. Manganese, *purple*; calcium, *yellow*; oxygen, *red*; D1, *green*; CP43, *pink*. *Data source* Umena et al. (2011)

$Mn_4CaO_5(H_2O)_4$ or $Mn_4CaO_4(OH)(H_2O)_4$ is formed through five oxygen atoms that act as oxo bridges linking the five metal atoms, and four water molecules that are bound to the Mn_4CaO_5 cluster and can generate O_2 (Fig. 6) (Umena et al. 2011; Yamanaka et al. 2012). Among the five metal and five oxygen atoms, three Mn, one Ca and four O form a cubane-like structure in which Ca and Mn occupy four corners and the O atoms occupy the other four. The fourth manganese (Mn4) is located outside the cubane; it is linked to Mn1 and Mn3 within the cubane by O5, and to O4 by a di-μ-oxo bridge (Umena et al. 2011). In this way, every two adjacent Mn atoms are linked by di-μ-oxo bridges: Mn1 and Mn2 via O1 and O3, Mn2 and Mn3 via O_2 and O3, and Mn3 and Mn4 via O4 and O5. The calcium is linked to all four Mn by oxo bridges: to Mn1 via the di-μ-oxo bridge formed by O1 and O5, to Mn2 via O1 and O2, to Mn3 via O2 and O5, and to Mn4 via the mono-μ-oxo bridge formed by O5 (Umena et al. 2011). It is also shown that four water molecules (W1 to W4) are associated with the Mn_4CaO_5 cluster, of which W1 and W2 are coordinated to Mn4 with respective distances of 2.1 and 2.2 Å, and W3 and W4 are coordinated to Ca with a distance of 2.4 Å. This suggests that some of the four waters may serve as the substrates for water oxidation (Umena et al. 2011).

Several studies are conducted to evaluate the functions of the PSI and PSII (Jordan et al. 2001; Dashdorj et al. 2004; Germano et al. 2004; Diner and Rappaport 2002; Li et al. 2006; Rappaport and Diner 2008; Müller et al. 2010; Nilsson Lill 2011; Schlodder et al. 2007, 2011; Nanba and Satoh 1987; Dekker and van Grondelle 2000; Greenfield and Wasielewski 1996; Klug et al. 1998; Prokhorenko and Holzwarth 2000; Byrdin et al. 2002; Yoder et al. 2002; Holzwarth et al. 2006).

4.1 Debates/Questions Regarding O_2-Releases from PSI and PSII

Some key issues on the debate concerning the details of electron- and O_2-release from PSI and PSII will be discussed in the following parts.

First, an electron is released upon excitation by light, either producing the charge-separated state $P680^+H_A^-$ from Chl molecules (P680), or accompanied by no charge separation (or by considerable protein relaxation) (Dashdorj et al. 2004; Germano et al. 2004; Rappaport and Diner 2008; Müller et al. 2010; Takahashi et al. 1987; Periasamy et al. 1978). Accordingly, after release of an electron by PSI or PSII upon excitation by light, is it possible to accept the same component of PSI or PSII? From the point of view of aquatic humic substances (fulvic and humic acids) or CDOM (DOM or FDOM, fluorescent dissolved organic matter), the answer is no. The secondary component (dissolved O_2 in water) can accept the electron to produce super oxide radical anion ($O_2^{\bullet -}$) and then H_2O_2 (Eqs. 3.36–3.40). The detailed mechanism for H_2O_2 production from DOM (or FDOM or CDOM) is extensively discussed in chapter "Photoinduced and Microbial Generation of Hydrogen Peroxide and Organic Peroxides in Natural Waters".

Second, which and how many Chl molecules are taking part to the primary donor sites in PSI and PS II? (Stewart et al. 2000; Jordan et al. 2001; Diner and Rappaport 2002; Li et al. 2006; Müller et al. 2010; Durrant et al. 1995; Dekker and van Grondelle 2000; van Gorkom and Schelvis 1993) The answer is that the first electron is released from the functional or chromophoric group bound to PSI or PSII, which is the easiest way to do it upon excitation by light. Subsequent electron releases occur in succession from the functional groups (for an analogy, see CDOM and FDOM, chapter "Colored and Chromophoric Dissolved Organic Matter in Natural Waters" and "Fluorescent Dissolved Organic Matter in Natural Waters"). It has been shown by fluorescence spectroscopy that longer-wavelength excitation is usually the first to take place, followed by the others. Therefore, Chl dimers or Chl molecules (generally with emission wavelengths >675 nm) bound to PSI or PSII are primarily responsible for excitation of electrons. In contrast, proteins or aromatic amino acid residues (generally having shorter emission wavelengths: <370 nm) are not excited in presence of Chl molecules upon irradiation (see also chapter "Fluorescent Dissolved Organic Matter in Natural Waters").

Third, why are PSI and PSII formed by a number of Chl molecules in their structure? It is assumed here that Chl *a* (or dimer Chl *a*) molecules are extremely photosensitive and can be excited by a small light intensity. Continuous H_2O_2 generation in the presence of little light is enabled by the occurrence of high numbers of Chl *a* molecules in PSI and PSII, which at the same time can contribute to the continuous photosynthesis in organisms and plants under light conditions. The factors affecting the generation of H_2O_2 (e.g. high or low light intensity, pH, nutrients and so on) can affect photosynthesis and induce structural modifications in PSI and PSII. For example, under intense light conditions there is an elevated production of H_2O_2, the excess of which can be photolytically converted into $HO^\bullet$. The hydroxyl radical can then degrade the proteins or amino acid residues. Such an effect can reduce the contents of proteins or amino acid residues, which are often observed in PSI and PSII (Neufeld et al. 2004; Shutova et al. 2005). The decomposition of proteins or amino acids (e.g. tryptophan) is also generally observed in sunlit water environments because of the effects of $HO^{\bullet}$ and other ROS (Mostofa et al. 2007, 2010, 2011; Moran et al. 2000).

Fourth, are there any O_2 or H_2O_2 molecules that may remain undetected among the 1,300 water molecules found in PSII? It is consistent to detect O_2 and H_2O_2 molecules in the PSII structure, which have often been observed in earlier studies. The occurrence of a large number of H_2O molecules suggests that O_2 may remain and be dissolved in those water molecules. Furthermore, H_2O_2 may be produced photolytically from O_2 as discussed before. Two facts may be responsible for not detecting O_2 or H_2O_2: (i) O_2 and H_2O_2 may disappear during the primary processing of the photosynthetic cells before examination; and (ii) former studies did not focus on the occurrence of H_2O_2 in PSII. In a recent study, it has been assumed that H_2O_2 may be “lost” amongst 1,300 H_2O molecules (Umena et al. 2011). The most likely reasons would be the structural similarity and the fact that H_2O_2 occurrence in the PSII structure was not expected. It should be noted that H_2O_2 may be decomposed to H_2O during the processing of photosynthetic cells for the determination of PS crystal structure.

It has been shown that two H_2O molecules in four reaction-center Chls are linked through H-bonding between water ligand and Chl_{D1} (Umena et al. 2011), and it may well be H_2O_2 that can make H-bonding in the proposed structure. It is also shown that two balls labeled I and II represent a single water molecule, disordered at two different positions separated by 1.8 Å. Position-I is able to H-bond to YD (redox-active tyrosine residue located at D2-tyr 160), whereas position-II is not able to H-bond to YD (Supplementary part) (Umena et al. 2011). On this basis, it can be assumed that H_2O_2 may occur in that structure instead of H_2O. Note that the bond length of O–O in H_2O_2 is 1.49 Å, which is larger than in the ground (triplet) state of molecular oxygen ($^3O_2$, 1.21 Å) (Abrahams et al. 1951). Among the 1300 H_2O molecules in each PSII monomer, a few of them are detected as disordered (Umena et al. 2011), a case in which the probability to mistakenly detect H_2O instead of H_2O_2 is relatively high. Future studies will be important to find out any presence of H_2O_2 instead of H_2O in the crystal structure of PSII.

The first two questions will be discussed comprehensively in the next section.

4.2 *Mechanism for Electron Transfer and O_2-Release in Photosystem II Reaction Centers*

Upon excitation by light, the electron release takes place at the central part of the reaction center (RC), at the primary donor P700 in PSI or P680 in PSII (Figs. 4, 5) (Müller et al. 2010; Nilsson Lill 2011; Umena et al. 2011). It is suggested that the

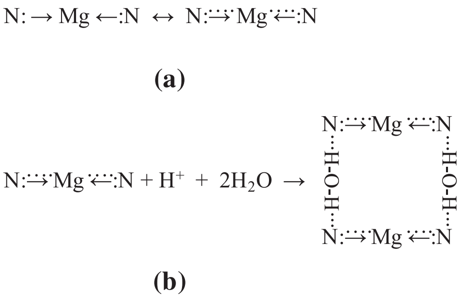


Fig. 7 The possible resonance configuration of Mg with π-electrons of two N-atoms located in the chlorophyll *a* structure (**a**) and chlorophyll *a* dimer (**b**). Only the two N-atoms in porphyrin ring with Mg are presented in the structure to simplify the resonance structure

primary electron release in PSII involves the chlorophyll *a* dimer (Boussaad et al. 1997; Nilsson Lill 2011). This can be justified by the theory of excitation of multiple functional groups bound to macromolecular organic substances (e.g. fulvic acids or humic acids). Light excitation is expected to induce first the release of the electron less strongly bound in the relevant functional groups, and then of the subsequent ones (see chapter "Colored and Chromophoric Dissolved Organic Matter in Natural Waters").

It is hypothesized that the first electron is released from the π-bonding system formed between two N-atoms in the porphyrin ring and Mg. In fact, Mg ($1s^2 2s^2 2p^6 3s^1 3p_x{}^1 3p_y{}^0 3p_z{}^0$) can form two covalent bonds with two N-atoms of the porphyrin ring using $3s^1$ and $3p_x{}^1$ orbitals, whilst other two empty $3p_y{}^0$ and $3p_z{}^0$ orbitals can accept the π-electrons from the remaining two N-atoms. The π-bonding systems among these orbitals ($3p_y$ and $3p_z$) can interchange with one another because of the similar energy levels. Therefore, one can have resonance configuration upon exchange of electrons between the orbitals and Mg (Fig. 7a). Chl *a* dimer is formed through hydrogen bonding via H_2O bridges, and H_2O is the key component in the formation of such dimers (Shipman et al. 1976; Hynninen and Lötjönen 1993; Boussaad et al. 1997; Catalan et al. 2004). It is supposed that hydrogen (H)-bonding is formed between the non-bonding π-electrons of two N-atoms in the porphyrin ring. The latter is also a resonance structure where electrons can move through the whole Chl *a* dimer (Fig. 7b).

The formation of H-bonds through H_2O bridges is suggested by earlier studies (Shipman et al. 1976), and can be justified by the shift of the π-bonding system in H–N–Mg–N–H (Fig. 7b). This system can assist the release of electrons in a much easier way than the single N–Mg–N system (Fig. 7a). Based on multimer model studies one obtains equal site energies and inhomogeneous widths for all pigments, which leads to similar distances and to nearest-neighbor dipole–dipole interactions between the central chlorin cofactors (Durrant et al. 1995; Renger and Marcus 2002; Barter et al. 2003). This may result into two wavelength positions for the electronic states in the reaction center (RC): uncoupled Chls can absorb at 670 nm, and electronically coupled chlorins (the central cofactors) or Chl dimers can absorb between 676 and 684 nm (Telfer et al. 1990; Durrant et al. 1995; Renger and Marcus 2002). Red shifts are commonly observed in in vitro Chl *a* systems, such as thin films, monolayers and colloidal dispersions, used as models for the in vivo system (Katz et al. 1991). It is known that red shifts occur when the release of electrons takes place in the functional groups that is bound to the component system (see also chapter "Colored and Chromophoric Dissolved Organic Matter in Natural Waters", "Fluorescent Dissolved Organic Matter in Natural Waters") (Mostofa et al. 2009; Senesi 1990). Note that Chl *a* has a broad absorption spectrum and can form dimers or aggregates through self assembly, which typically leads to changes in its optical properties (Shipman et al. 1976; Hynninen and Lötjönen 1993; Closs et al. 1963; Katz et al. 1963; Fong 1974; Shipman et al. 1975; Katz 1990, 1994; Frackowiak et al. 1994). Formation of the dimer often occurs through H-bonding in the N-heterocyclic base pair (Catalan et al. 2004), which can support the occurrence of H-bonding between N and H_2O (Fig. 7b).

Two possible hydrogen bonds were also discussed in earlier studies. First, formation of H-bonds might occur between central Mg and H_2O according to the $Mg\ldots OH_2$ interaction (Hynninen and Lötjönen 1993). Second, the keto carbonyl group of Chl a may participate in the formation of Chl a dimers, either through coordination with Mg or through H-bonding of the H–X type, where X = O, N and S (Shipman et al. 1976; Closs et al. 1963; Katz et al. 1963; Fong 1974; Shipman et al. 1975; Katz 1990). However, these two previous assumptions are not possible electronically because the outer shells of Mg are entirely full, after bonding with two covalent bonds and two unpaired π–electron systems with four N-atoms of the Chl *a*. Therefore, Mg has less probability to accept further electrons or H-bonding with other groups. Moreover, the formation of such proposed bonding systems is not consistent with the easiest way of electron release via absorption in the longer wavelength region.

Crystal structures of the reaction center have identified two chlorophyll monomers forming a dimer with a partial structural overlap, which are thus stabilized by van der Waals interactions (Nilsson Lill 2011). The structure of the chlorophyll dimer has been optimized using dispersion-corrected density functional theory (B3LYP-DCP) and it has been found that the dimerization energy is approximately -17 kcal mol^{-1} (Nilsson Lill 2011). Electrons may be rapidly released from these resonance configurations upon irradiation of the Chl *a* dimmer, according to the proposed dimer formation (Fig. 6). This can be understood from the interaction mechanism between the functional group [$–CH_2–(NH_3^+)–CH–COO^-$] in tryptophan [$C_8H_5(NH)\text{-}CH_2(NH_3^+)CHCOO^-$] and metal ions, where the functional group [$–CH_2\text{-}(NH_3^+)–CH–COO^-$] can display resonance configuration that is responsible for the longer wavelength fluorescence emission spectra (see chapter "Complexation of Dissolved Organic Matter With Trace Metal Ions in Natural Waters").

PSII acts as one component and upon irradiation, the released electron may not accept the same component of PSII that can be understood from aquatic ecosystem. For example, in aqueous media fulvic acid or humic acid upon irradiation can donate the electron to O_2 and form $O_2^{\bullet-}$ and then H_2O_2, which is a well-accepted mechanism by all aquatic scientists. Therefore, it is hypothesized that the released electron in PSII may react with other components present in the cells, the most efficient of which is O_2 that can form $O_2^{\bullet-}$ and then H_2O_2. The latter species are often detected in cells as discussed in the earlier sections. It is also established that H_2O_2 formation is the primary step of many photoinduced processes in aqueous solution that finally lead to the formation of the $HO^{\bullet}$ radical (see chapter "Photoinduced and Microbial Generation of Hydrogen Peroxide and Organic Peroxides in Natural Waters").

Upon excitation, an electron is transferred from the Chls to the Pheo HA, producing the charge-separated state $P680^+H_A^-$ as assumed by earlier studies (Germano et al. 2004; Rockley et al. 1975; Thurnauer et al. 1975; Shuvalov and Klevanik 1983; Kirmaier and Holten 1987; Holzapfel et al. 1990). Similarly, in PSI a primary charge separation occurs in the P700 reaction center that can lead to the reduction of A_0 (two chlorophylloid primary electron acceptors), creating the radical ion pair $P700^+A_0^-$ (Krauß 2003; Brettel 1997; Müller et al. 2010; Webber and Lubitz 2001; Fromme et al. 2001). However, no concrete evidence has been found for the formation of these types of radicals in PSI or PSII. Rather, experimental studies support the idea that primary electron transfer reactions are accompanied by molecular readjustments or reorganizations involving pigments and proteins, or the interaction of pigment-protein complexes in the reaction center (Dashdorj et al. 2004; Kleinfeld et al. 1984; Woodbury and Parson 1984; Kirmaier et al. 1985a, b; Holten et al. 1986; Kirmaier et al. 1986; Tiede et al. 1987; Mullineaux et al. 1993; Savikhin et al. 2001; Karapetyan 2004).

It is also observed that chlorophyll-binding PsbS protein (22-kD protein of PSII), which belongs to the family of light-harvesting proteins, can contribute only to quenching but not to light harvesting (Li et al. 2000, 2002; Aspinall-O'Dea et al. 2002; Bergantino et al. 2003). Indeed, the degree of fluorescence quenching in vivo can correlate with the content of PsbS (Li et al. 2004). Dissipation of energy in PSI trimers of cyanobacteria takes place with a contribution of the long-wavelength chlorophyll, and the excited state of which is quenched by the cation radical of P700 or by P700 in its triplet state (Karapetyan 2004). The low fluorescence yield of Chls in light-harvesting antenna complexes is indicative of an additional pathway of energy dissipation in oligomers, which would protect the PSII complex of cyanobacteria against photodestruction (Karapetyan 2004).

It can thus be hypothesized that excitation followed by charge transfer could produce $P680^+O_2^{\bullet-}$ instead of $P680^+H_A^-$. O_2 is the primary acceptor for excited electrons in aquatic media and is involved in the production of H_2O_2 as discussed earlier. This result is supported by Laser flash photolysis studies, in which a charge-transfer excited state has not been detected from the spectra. Recovery kinetics, including observation of both triplet decay and ground-state folding reactions, show that the flash transient obtained from the pinned form consists of a triplet and of a ground state moiety in the unpinned configuration (Periasamy et al. 1978). Experimental optical data and structure-based simulations showed nanosecond absorption dynamics at ~685 nm, after excitation of PS I from *Synechocystis* sp. PCC 6803. It is suggested that the electrochromic shift of absorption bands of the Chl *a* pigments may occur around the secondary electron acceptor, through considerable protein relaxation (Dashdorj et al. 2004; Savikhin et al. 2001).

A recent study has shown that the PSII monomer consists of 1300 H_2O molecules, a few of which have been detected as disordered (Umena et al. 2011). H_2O_2 was not considered as a component of PSII structure in that study. Concurrently, four successive photoinduced turnovers provide the WOC with four oxidising equivalents and drive it through an S-state cycle, with S-states ranging from S_0 to S_4 and O_2 is being released on the S_3 to S_4 transition.

Now the questions are: how is it possible for H_2O to undergo photodissociation through four successive photoinduced turnovers, needing energy in the presence of H_2O_2 that can easily be decomposed and produce O_2? How can H_2O in a cell accept four consecutive electrons in the presence of many additional components including O_2 that can more easily accept electrons? Under these conditions, the easiest pathway would be the addition of one electron to O_2 with formation of $O_2^{\bullet -}$ and then of H_2O_2. This is a well established mechanism in water media and could take place in photosynthetic cells as well. Note that the main radiation absorbers in natural waters are chromophoric (or colored) DOM (CDOM) (10–98 %), phytoplankton or chlorophyll (32–85 %), H_2O (0.3–9 % in the red portion of the visible spectrum, depending on water being clear or turbid) and so on (see chapter "Colored and Chromophoric Dissolved Organic Matter in Natural Waters"). It is entirely impractical to consider that H_2O can accept four successive electrons under light condition in the presence of O_2 or other organic components in a photosynthetic cell and there is no evidence in that regards.

It is therefore theorized that

> if H_2O would decompose by the reaction with CO_2 in photosynthesis, then all H_2O would convert into O_2 by organisms and plants after the origin of life on earth to date and no H_2O would remain in the biosphere. Instead of H_2O, photoinduced generation of H_2O_2 from dissolved O_2 in water bound in photosynthetic cells (3.33–3.39) is reacted with CO_2 in photosynthesis that can limit the photosynthesis under light condition.
> Then further conversion of H_2O_2 to O_2 either through photosynthesis [$xCO_2(H_2O) + yCO_2(H_2O) \rightarrow C_x(H_2O)_y + O_2 + E\ (\pm)$] or both photolytically ($2H_2O_2 + h\upsilon \rightarrow O_2$ + unknown oxidant) and biologically ($2H_2O_2$ + catalases/peroxidases $\rightarrow O_2 + 2H_2O$) may balance the environment.

This can be supported by the observation of several phenomena:

(i) Formation and occurences of H_2O_2 in photosynthetic cells of organisms through production of $O_2^{\bullet -}$ from whole bacteria of several species, from phagocytic cells, from spermatozoa as well as peroxisoms, mitochondria and chloroplasts (Komissarov 2003; Bach 1894; Chance et al. 1979; Halliwell 1981; Holland et al. 1982; Wilhelm et al. 1996, 1997, 1999; Halliwell and Gutteridge 1999; López-Huertas et al. 1999; Baker and Graham 2002; del Río et al. 2006; Krieger-Liszkay et al. 2008; Lyubimov and Zastrizhnaya 1992a, b; Turrens 1997; Karuppanapandian et al. 2011). (ii) Releases of O_2 from H_2O_2 during photosynthesis are evidenced in earlier studies (Komissarov 1994, 2003; Velthuys and Kok 1978; Asada and Badger 1984; Asada and Takahashi 1987; Mano et al. 1987; Renger 1987; Anan'ev and Klimov 1988; Bader and Schmid 1988, 1989; Schroeder 1989; Schröder and Åkerlund 1990; Miyake and Asada 1992; Kuznetsov et al. 2010; Bernardini et al. 2011; Yin et al. 2006). (iii) The

O_2-releases [H_2O_2 + light or enzymes (catalases/peroxidases) → O_2 + $2H_2O$ or other components] and their reused in H_2O_2 generation in photosynthetic organisms ($O_2 + \text{Chl} + H^+ + h\upsilon \rightarrow H_2O_2$) can balance the O_2 level in the environments in new photosynthetic reaction. But this does not occur in old photosynthetic reaction. (iv) Conversion of H_2O_2 to O_2 occurs at a higher extent in biological systems than in photoinduced decomposition processes (Moffett and Zafiriou 1990). For instance, the Cu(II) bathocuproinedisulfonic acid complex ($Cubc_2$) can convert H_2O_2 to O_2 via the reaction (Eq. 4.1) (Moffett et al. 1985):

$$2\text{Cu(II)bc}_2 + H_2O_2 \rightarrow 2\text{Cu(I)bc}_2 + O_2 + 2H^+ \tag{4.1}$$

Unconvincing evidence has been found for S_0 to S_4 transitions, and four successive transitions are needed for H_2O decomposition (Rappaport and Diner 2008; Kok et al. 1970; Joliot and Kok 1975; Krishtalik 1986, 1990).

(v) It is hypothesized that the O–O bond formation occurs when O5 in Mn_4CaO_5 cluster provides one O atom via formation of hydroxide ion in the S_1 state (Umena et al. 2011; Saito et al. 2012). A major issuer is then if it is possible to break down O5 in the Mn_4CaO_5 cluster. The problem is that, were it possible, probably the entire PSII system would be broken down. Furthermore, each Mn atom in the Mn_4CaO_5 cluster is in octrahedral form with six ligands, and it is also paramagnetic with 5 unpaired electrons in its outer *d*-orbitals ($Mn^{2+} = 1s^2 2s^2 2p^6 3s^2 3p^6 4s^0 3d^5$). The result is that Mn could carry out strong H-bonding with other components. Such an effect enables a second coordination sphere by D1-Asp 61, D1-His 337 and CP43-Arg 357, in addition to the direct ligands. Therefore, these three residues might be responsible for maintaining the oxygen-evolving activity (Umena et al. 2011; Nixon and Diner 1994; Chu et al. 1995; Hwang et al. 2007; Service RJ, Hillier W, Debus RJ 2010). D1-Asp 61 is located at the entrance of a proposed proton exit channel involving a chloride ion (Cl^-) in Mn_4CaO_5 (Umena et al. 2011; Kawakami et al. 2009; Guskov et al. 2009; Murray and Barber 2007; Ho and Styring 2008). This residue may facilitate proton exit from the Mn cluster. Proton releases from Mn_4CaO_5 may play a key role in the formation of H_2O_2 via $O_2^{\bullet-}$ and $HO_2^{\bullet}$.

(vi) Finally, the occurrence of about 1,300 water molecules in the PSII monomer, located at the luminal and stromal sides (Umena et al. 2011), could allow the inclusion of a lot of dissolved O_2 molecules. They could add electrons after they are released from Chl molecules upon excitation by light. Crystal structures of PSI or PSII do not include any information about dissolved O_2, and issue that will need further studies to be clarified.

5 Factors Affecting the Photosynthesis of Organisms

Cyanobacteria carry out oxygenic photosynthesis using a photosynthetic system similar to that observed in chloroplasts of higher plants. Therefore, cyanobacteria can be used in model studies to understand the effects of various environmental factors

(Allakhverdiev and Murata 2008; Pfenning 1978; Öquist et al. 1995). However, the anti-oxidant systems in cyanobacteria are significantly different from those of higher plants (Asada 2006; Demmig-Adams and Adams III 1992, 2002). This can vary the effects of various environmental stresses on cyanobacteria, bacteria and higher plants.

Studies show that terrestrial plants are adapted to their annual life cycles of growth, reproduction and senescence. Compared to the annual climate cycle, phytoplankton biomass can turn over around 100 times a year as a result of fast growth and equally fast consumption by grazers (Calbet and Landry 2004; Behrenfeld et al. 2006; Winder and Cloern 2010). It has been observed that the timing of these life-history transitions can vary among species and among regions with variation in temperature and sunlight intensity (Winder and Cloern 2010; Myneni et al. 1997; Menzel and Fabian 1999; Peñuelas and Filella 2001; Jolly et al. 2005; White et al. 2009; Richardson et al. 2010). Correspondingly, annual phytoplankton cycles can differ across ecosystems, because of year to year variability and with changes in the climate system (Winder and Cloern 2010; Garcia-Soto and Pingree 2009; Thackeray et al. 2008; Paerl and Huisman 2008; McQuatters-Gollop et al. 2008; Cloern and Jassby 2008; Winder and Schindler 2004; Edwards and Richardson 2004; Scheffer 1991; Pratt 1959). These periodic cycles can be linked with annual fluctuations of mixing, temperature, light, precipitation and with other drivers of population variability, including human disturbance. There are also effects from periodic weather events and strong trophic coupling between phytoplankton and their consumers (Winder and Cloern 2010; Smetacek 1985; Sommer et al. 1986; Cloern 1996).

Cyanobacteria can control a variety of environmental stressors such as UV light, heat, cold, drought, salinity, nitrogen starvation, photo-oxidation, anaerobiosis and osmotic stress, by developing a number of defence mechanisms (Fay 1992; Tandeau de Marsac and Houmard 1993; Sinha and Häder 1996). The most important one is the production of photoprotective compounds such as mycosporine-like amino acids (MAAs) and scytonemin (Sinha et al. 1998, 1999a, b; 2001); availability of enzymes such as superoxide dismutase, catalase and peroxidase (Burton and Ingold 1984; Canini et al. 2001); repair of DNA damage (Sinha and Häder 2002) and synthesis of shock proteins (Sinha and Häder 1996; Borbely and Suranyi 1988; Bhagwat and Apte 1989).

Organisms are thus affected by several factors that could either increase or decrease their photosynthetic and respiratory activities (Doyle et al. 2005; Nozaki et al. 2002; Shimura and Ichimura 1973; Pope 1975; Pick and Lean 1987; Babin et al. 1996; Shapiro 1997; Hyenstrand et al. 1998; Elser 1999; Dokulil and Teubner 2000; MacIntyre et al. 2000; Xie et al. 2003; Qu et al. 2004; Tank et al. 2005; Wängberg et al. 2006; Sobrino et al. 2008). The key factors affecting these activities are mostly documented on the basis of the growth and development of organisms. Such factors are: (i) seasonal variation in sunlight and UV radiation, which affect photosynthesis; (ii) occurrence of CO_2 forms (dissolved CO_2, carbonic acid, bicarbonate, carbonate); (iii) variation in temperature; (iv) water stress (drought) and precipitation/rainfall; (v) contents and nature of DOM and POM; (vi) nutrient availability; (vii) variation in trace metal ions; (viii) salinity or salt stress; (ix) presence of toxic pollutants; (x) effect of size-fractionated phytoplankton; (xi) global warming.

5.1 Seasonal Variation in Sunlight and UV Radiation on Photosynthesis

Solar radiation is the key driving force for the occurrence of photosynthesis in natural waters (Sinha et al. 2001; Rastogi et al. 2010; Jiang and Qiu 2011; Sobek et al. 2007). Exposure of photosynthetic organisms to strong light (or UV light) can significantly inhibit the PSII activity, with resulting photoinhibition of or photodamage to PS II (Aro et al. 1993; Melis 1999; Andersson and Aro 2001; Han et al. 2001; Nishiyama et al. 2001, 2008; Adir et al. 2003). Photoinhibition of photosynthesis is a process by which excessive irradiance, absorbed by the leaves, can inactivate or impair the chlorophyll-containing reaction centers of chloroplasts, thus inhibiting photosynthesis (Bertamini et al. 2006). Because of the differences among the organisms, the effects of light can be classified into two sections (aquatic microorganisms and higher plants) for their better understanding.

Effects of Sunlight on Aquatic Microorganisms

Cyanobacteria or phytoplankton cells can utilize photosynthetically active radiation (PAR, 400–700 nm) to drive photosynthesis within the euphotic zone (see also global warming chapter "Impacts of Global Warming on Biogeochemical Cycles in Natural Waters") (Smith and Baker 1979; Abboudi et al. 2008; Li et al. 2011). Solar UV-A radiation (315–400 nm) acts as an additional source of energy for photosynthesis to enhance the CO_2 fixation in tropical marine phytoplankton (Li et al. 2011; Gao et al. 2007, 2007). However, UV-A does not bring any enhancement to carbon fixation in pelagic water (Li et al. 2011). The cells of aquatic microorganisms can be exposed to ultraviolet radiation (UVR, 280–400 nm), which can penetrate up to 60 m into the pelagic water column (Smith and Baker 1979). Furthermore, depletion of the stratospheric ozone layer can cause additional penetration of UV radiation in the Arctic and Antarctic regions. Such a phenomenon has detrimental effects on the processes involved in primary production (see also chapter "Impacts of Global Warming on Biogeochemical Cycles in Natural Waters") (Huisman et al. 2006; Häder et al. 2007; Zhang et al. 2007). Solar UV-B (280–315 nm), and partly UV-A (315–400 nm) can reduce growth and photosynthetic rates, increase permeability of cell membranes, damage proteins or DNA molecules, pigments, and even lead to cell death (see also chapter "Impacts of Global Warming on Biogeochemical Cycles in Natural Waters") (Jiang and Qiu 2011; Wängberg et al. 2006; Behrenfeld et al. 1993; Sass et al. 1997; Campbell et al. 1998; Rajagopal et al. 2000; Helbling et al. 2001; He and Häder 2002; Buma et al. 2003; Sobrino et al. 2004; Litchman and Neale 2005; Wu et al. 2005; Bouchard et al. 2006; Agusti and Llabrés 2007; Rath and Adhikary 2007; Gao et al. 2008; Pattanaik et al. 2008; Jiang and Qiu 2005).

It has been shown that, ranging from coastal (case 1) to pelagic (case 2) surface seawaters, UV-B can cause similar inhibition whilst the inhibition of photosynthesis by UV-A (315–400 nm) increases when passing from coastal to offshore waters (Li et al. 2011). UV-B inhibits photosynthesis up to 27 % and UV-A up to 29 %. It has also been shown that the daily integrated inhibition by UV-A can reach 4.3 % and 13.2 %, whilst that by UV-B can reach 16.5 % and 13.5 % in coastal and offshore waters, respectively (Li et al. 2011). Additionally, exclusion of UV radiation can increase photosynthesis by 10–65 % in algae from the Mediterranean, 17–46 % in intertidal algae from southern Chile, and 15–20 % in algae (*Laminaria Saccharina*) from the North Sea (Hanelt et al. 1997; Jiménez et al. 1998; Gómez et al. 2004).

UV-stimulated inorganic carbon acquisition is often observed in phytoplankton species (Beardall et al. 2009; Wu and Gao 2009). Phytoplankton cells grown in nutrient replete conditions are more resistant to solar UV radiation, and also their contents of UV-absorbing compounds increases (Marcoval et al. 2008). Microplankton (>20 m) are more plentiful in coastal waters, while picoplankton (<2 m) are more abundant in open oceans (Marañón et al. 2001; Ho et al. 2008). In terms of their responses to UV, large cells are capable of synthesizing and accumulating UV-absorbing compounds that play a protective role against UV. These screening compounds are not found in picoplankton cells (Raven 1991; Garcia-Pichel 1994) that, therefore, would be more sensitive to solar UV. This issue is partially offset by a much faster repair process of damaged DNA (Helbling et al. 2001; Callieri et al. 2001). Because taxonomic composition, accumulation of UV-absorbing compounds and nutrient availability are typically different, physiological responses of phytoplankton assemblages to solar UV can differ geographically from coastal to pelagic waters (Li et al. 2011).

Cyanobacteria are important and ubiquitous prokaryotes that populate terrestrial and aquatic habitats, and they are important contributors to global photosynthetic biomass production (Whitton and Potts 2000). Enhanced UV-B radiation can affect cyanobacterial growth, photosynthetic efficiency, pigments, morphology, as well as cell size and shape. Anyway, different responses are observed in different species exposed to different UV doses (Wu et al. 2005; Rath and Adhikary 2007; Pattanaik et al. 2008; Jiang and Qiu 2005; Harrison and Smith 2009). It has also been shown that exposure to UV radiation can reduce the activity of alkaline phosphatase, a common extracellular enzyme, by up to 57 %. Interestingly, it is more often decreased under ultraviolet A than ultraviolet B exposure (Tang et al. 2005). As already mentioned, algal nutritional status can influence the UV radiation sensitivity but, on the other hand, UV radiation can inhibit uptake and assimilation of inorganic nutrients (Harrison and Smith 2009). This is likely caused by the rapid UV radiation-induced changes of nitrate into $HO^{\bullet}$ and $^{\bullet}NO_2/NO_2^-$, which may reduce the availability of NO_3^- for primary production (see chapter "Photoinduced Generation of Hydroxyl Radical in Natural Waters").

It is estimated that, depending on location, ambient UV radiation can reduce carbon fixation rates up to 65 % in surface waters of the Antarctic region, down to undetectable levels at 36 m (Boucher and Prezelin 1996). On average, up to 42 % of primary production inhibition in the water column is carried out by UV radiation on a daily basis outside the ozone hole (Wängberg et al. 2006; Harrison and Smith 2009; Helbling et al. 1992; Smith et al. 1992; Holm-Hansen et al. 1993; Bertoni et al. 2011). In contrast, during a ozone hole depletion event, the inhibition is increased to ~50 %. This can be supported by the experimental observations that UV-B radiation can inhibit the oxygen-evolving complex of PSII in *M. aeruginosa* (Jiang and Qiu 2011). The whole electron-transport activities are significantly varied: the transfer from water to methyl viologen being inhibited by 27.9 % under UV-B, that from diphenylcarbazide to methyl viologen by 13.3 % (Jiang and Qiu 2011).

Cyanobacterial blooms in freshwater have apparently increased over the last few decades all over the world (Xu et al. 2000; Chen et al. 2003; McCarthy et al. 2007). UV-B influences the CO_2-uptake mechanism of M. *aeruginosa*, and this cyanobacterium has many adaptive strategies to cope with prolonged UV-B exposure (Jiang and Qiu 2005; Song and Qiu 2007). It has been shown that maximum quantum yield and maximum electron transport rate in seaweeds collected from the Red Sea decreased largely due to the combined effects of increased irradiance (PAR) and presence of UV radiation (Figueroa et al. 2009). A 33-kDa protein of the water-splitting complex is sensitive to UV-B. Therefore, its degradation contributes importantly to the decline of the electron transport rate (Jiang and Qiu 2011; Prabha and Kulandaivelu 2002). Short-term UV-B exposure can severely inhibit photosynthetic capability, which could be quickly restored upon exposure to PAR (Jiang and Qiu 2011). Quite surprisingly, UV-A can assist the photo repair of UV-damaged DNA and enhance carbon fixation under reduced levels of solar radiation or fast mixing conditions (Gao et al. 2007, 2007; Karentz et al. 1991; Barbieri et al. 2002; Helbling et al. 2003). Recent study reveals that the PSII of *M. aeruginosa* FACHB 854 is more sensitive to UV-B exposure than PSI, and the oxygen-evolving complex of PS II is an important target for UV-B damage (Jiang and Qiu 2011).

The mechanisms behind the photoinhibition effects of strong sunlight, UV light or high irradiance (drought/heat stress) on aquatic microorganisms are presumably involving two facts: First, there are direct effects in which a high number of electrons is released from chlorophylls (Chl) (P680) in PSII of microorganisms, upon excitation by strong light or strong UV light (Eq. 5.1). The release of many electrons can produce elevated amounts of reactive oxygen species (ROS) such as ${}^1O_2$, $O_2^{\bullet-}$, H_2O_2 and $HO^\bullet$ (Eq. 5.2). Among the ROS, H_2O_2 can be used in photosynthesis whilst the remaining ROS including H_2O_2 can react with the Chl^+ ($P680^+$) functional groups bound to PSII, killing the cells (Eq. 5.3). These reactions can be schematically depicted as follows:

$$\mathrm{Chl\ (or\ P680)} + h\upsilon \rightarrow \mathrm{Chl}^+ \left(\mathrm{or\ P680}^+\right) + e^- \tag{5.1}$$

$$e^- + O_2 + h\upsilon \rightarrow {}^1O_2/O_2^{\bullet-}/H_2O_2 + h\upsilon \rightarrow HO^\bullet \tag{5.2}$$

$$HO^\bullet \left({}^1O_2/O_2^{\bullet-}/H_2O_2\right) + \mathrm{Chl}^+ \left(\mathrm{or\ P680}^+\right) \rightarrow \mathrm{Chl}^+ \left(\mathrm{or\ P680}^+\right)\mathrm{\ damage} \tag{5.3}$$

ROS production in cells of aquatic microorganisms has generally been detected in earlier studies, which are extensively discussed in earlier sections. The process is supported by the earlier observation that chlorophylls can easily undergo photooxidation, involving attack of singlet oxygen and enzymatic degradation (Brown SB and Hendry 1991; Gossauer and Engel 1996). Experimental studies show that H_2O_2 can affect the cyanobacterium at 10 times lower concentrations than green alga and diatom, and a strong light-dependent toxicity can enhance the difference (Drábková et al. 2007).

Second, indirect effects can be operational by which UV or strong light can produce a significant amount of strong oxidizing agents. For instance, $HO^{\bullet}$ can be photolytically generated in the presence of H_2O_2 (photo-Fenton raction or direct photodissociation), hydrogen peroxide being produced by DOM (of both algal and terrestrial origin). The hydroxyl radical can also be photoproduced by other chemical species such as NO_2^- and NO_3^- (see the chapters "Dissolved Organic Matter in Natural Waters", "Photoinduced and Microbial Generation of Hydrogen Peroxide and Organic Peroxides in Natural Waters", "Photoinduced Generation of Hydroxyl Radical in Natural Waters" and "Photoinduced and Microbial Degradation of Dissolved Organic Matter in Natural Waters" for a detailed description). The $HO^{\bullet}$ radical would subsequently react with the functional groups present in the cells of aquatic microorganisms. The indirect effect may significantly affect waters with high contents of DOM and POM, which are usually associated to elevated production of photo- and microbial products and, as a consequence, to high photosynthesis and high primary production. Moreover, it has been shown that the production of $HO^{\bullet}$ during an ozone hole (151 Dobson units) is enhanced by at least 20 %, mostly from nitrate photolysis and to a lesser extent from DOM photoinduced reactions, in Antarctic seawater. Similar results have been observed for Arctic water (see chapters "Photoinduced and Microbial Generation of Hydrogen Peroxide and Organic Peroxides in Natural Waters" and "Photoinduced and Microbial Degradation of Dissolved Organic Matter in Natural Waters" for detailed description) (Rex et al. 1997; Qian et al. 2001; Randall et al. 2005).

Note that cyanobacteria (or phytoplankton) can produce autochthonous DOM including autochthonous fulvic acids, which are very efficient in the production of H_2O_2 (and of $HO^{\bullet}$ as a consequence under irradiation). Regeneration of autochthonous DOM and nutrients $\left(NO_3^-,\ NO_2^-,\ PO_4^{3-} \text{and } NH_4^+\right)$ occurs during the photoinduced and microbial assimilation of cyanobacteria or phytoplankton, and simultaneously also from the photoinduced degradation of DOM in natural waters (see chapter "Dissolved Organic Matter in Natural Waters", "Photoinduced and Microbial Generation of Hydrogen Peroxide and Organic Peroxides in Natural Waters", "Photoinduced Generation of Hydroxyl Radical in Natural Waters", and "Impacts of Global Warming on Biogeochemical Cycles in Natural Waters" for detailed description). High solar irradiation generally induces the production of large amounts of H_2O_2 and $HO^{\bullet}$, from DOM or NO_2^- and NO_3^- in aqueous media (see also the chapters "Photoinduced and Microbial Generation of Hydrogen Peroxide and Organic Peroxides in Natural Waters" and "Photoinduced Generation of Hydroxyl Radical in Natural Waters") (Mostofa and Sakugawa 2009; Takeda et al. 2004). Moreover, light plays a significant role in the cycling of terrestrially-derived DOM and (to a certain extent) of autochthonous DOM. It can potentially increase metabolism of both terrestrially and microbially derived DOM in natural waters (Hiriart-Baer et al. 2008). Low light levels, due to increased CDOM, do not have significant effects on the benthic microfloral community at mid-shelf locations (Darrow et al. 2003).

Enhanced solar UV-A (315–400 nm) and/or UV-B radiation (280–315 nm) can reduce growth and photosynthetic rates, inhibit pigment production, increase permeability of cell membranes, damage proteins or DNA molecules, and even lead to cell death (see chapter "Impacts of Global Warming on Biogeochemical Cycles in Natural Waters" for more references) (Jiang and Qiu 2011). At normal ozone concentrations (i.e. 344 Dobson Units), UV radiation can reduce primary productivity in surface waters by as much as 50 % (see chapter "Impacts of Global Warming on Biogeochemical Cycles in Natural Waters" for more references) (Cullen and Neale 1994). A normal level of UV radiation also reduces phytoplankton production by 57 % at a depth of 1 m, while such inhibition decreases to <5 % at 30 m, at 50ºS in mid December (Arrigo 1994). Such effects on aquatic organisms might be caused directly by UV radiation and indirectly through high production of $HO^\bullet$ in epilimnetic (upper layer) waters. Both effects are able to alter the structural configuration of organisms with release of many organic substances in epilimnetic (surface layer) waters (see chapter "Impacts of Global Warming on Biogeochemical Cycles in Natural Waters" for more references) (Mostofa et al. 2009; Mostofa et al. 2009; Rastogi et al. 2010; Ingalls et al. 2010). Some studies also hypothesize that the primary target of photodamage to PSII by strong light is the PSII reaction center. A primary event in photoinhibition could be the damage to the D1 protein, which activates its rapid degradation by several proteases (Aro et al. 1993; Andersson and Aro 2001; Nishiyama et al. 2008; Kanervo et al. 1993; Tyystjärvi et al. 2001). Studies show that hydroperoxides (H_2O_2 and organic peroxides, ROOH) are often considered as indicators of membrane damage (see also chapter "Photoinduced and Microbial Generation of Hydrogen Peroxide and Organic Peroxides in Natural Waters") (Hagege et al. 1990a, b).

Effects of Sunlight on Higher Plants

High irradiance can affect the PSII activity, with negative effect on the PSII-mediated electron transport rate, disarrangement of PSII system, degradation of the D1 protein and/or its metabolism in a circadian-dependent manner (the same issue could also involve various polypeptides) (Aro et al. 1993; Pandey and Yeo 2008; Maslenkova et al. 1995; Rintamäki et al. 1995; Baena–González and Aro 2002; Booij-James et al. 2002; Hofman et al. 2002; Henmi et al. 2003, 2004; Nováková et al. 2004; Porta et al. 2004; Suzuki et al. 2004; Szilárd et al. 2007). The final result is a decrease of the photosynthetic capacity of plants. The decrease in photosynthetic efficiency is mostly associated with three facts: First, the decline in the enzymatic reactions of the Calvin–Benson cycle (Friedrich and Huffaker 1980); second, the decrease in the light reactions, i.e. the photoinduced reactions of PSI and PSII (Grover and Mohanty 1992; Wingler et al. 2004); and third, the changes in the structure of chloroplasts (Tang et al. 2005). UV-B sensitivity depends on the oxidation state of the water-splitting complex of PS II in higher plant such as spinach (Szilárd et al. 2007). It has been shown that ROS produced endogeneously under high-irradiance conditions can cause more deleterious effect in the decrease of PSII-mediated electron transfer rate, compared with exogenously applied H_2O_2 and $^{\bullet}OH$ stresses (Pandey and Yeo 2008). Strong illumination of thylakoid membranes in the absence of an acceptor can results in oxygen accepting electrons and subsequently producing reactive oxygen species, ROS (Pandey and Yeo 2008).

The photoproduction rate of ROS is largely enhanced under conditions where photon intensity is in excess of that required for the CO_2 assimilation (Asada 2006). It has been shown that the quantum yield of PSII is increased more rapidly than CO_2 assimilation in 20 % O_2, which can result from the electron flux through the water–water cycle (Makino et al. 2002). This flux can reach a maximum just after illumination, and can rapidly produce non-photoinduced quenching. With increasing CO_2 assimilation, the electron flux of water–water cycle and the non-photoinduced quenching is decreased (Makino et al. 2002). The cyclic electron flow around PSI can produce non-photoinduced quenching, which remains at elevated levels upon switching to low oxygen (2 % O_2) (Makino et al. 2002). The water–water cycle is thus believed to dissipate the energy of excess photons (Asada 1999, 2000, 2006; Foyer and Noctor 2000; Osmond 1997; Osmond and Grace 1995;). Such a cycle is defined as the process of the electron flow from water in PSII to water in PSI (Asada 1999). In addition, H_2O_2 and ROS can directly be produced by excited PSII under photoinhibitory conditions that trigger the turnover of the D1 protein (see also earlier sections) (Aro et al. 1993; Prasil et al. 1992; Bradley et al. 1991). ROS can influence the outcome of photodamage, primarily via inhibition of translation of the *psbA* gene, which encodes the precursor of the D1 protein (Nishiyama et al. 2001). The rate of photo-damage is proportional to irradiance (Pandey and Yeo 2008).

The mechanism behind the high irradiance (or heat stress or high temperature or drought) effect on higher plant is the similar to that explained before for cyanobacteria or phytoplankton in aqueous media. However, in higher plants the reaction centers of PSI and PSII in chloroplast thylakoids are the major ROS generation site. Photoreduction of O_2 to H_2O_2 occurs in PSI (Mehler 1951): the primary reduced species is the superoxide radical anion $\left(O_2^{\bullet-}\right)$, and its disproportionation produces H_2O_2 and O_2 (Asada et al. 1974). Correspondingly, ground (triplet) state oxygen $\left({}^3O_2\right)$ in PSII is excited to singlet state $\left({}^1O_2\right)$ by the triplet state of chlorophyll (Hideg et al. 1998; Telfer et al. 1994). The mechanism behind the photoreduction of O_2 in PSI of higher plants according to Asada (Asada 2006) and other studies (Lobanov et al. 2008; Parmon 1985; Bruskov and Masalimov 2002) can be expressed as follows (Eqs. 5.4–5.11):

$$\text{P680 or P700} + h\upsilon \rightarrow e^- + \text{P680}^+ \text{or P700}^+ \quad (5.4)$$

$$O_{2(aq)} + e^- + h\upsilon \rightarrow O_2^{\bullet-}\ (\text{PSI}) \quad (5.5)$$

$$2O_2^{\bullet-} + 2H^+ \rightarrow H_2O_2 + O_2 \quad (5.6)$$

$$H_2O_2 + 2\text{AsA} \rightarrow 2H_2O + 2\text{MDA} \quad (5.7)$$

In this modified mechanism, the electron is originated mostly from photoinduced excitation of both P680 and P700 (Eq. 5.4). Dissolved O_2 in water is thus reduced photolytically, differently from the results of earlier studies. The disproportionation of O_2^- to H_2O_2 and O_2 is catalyzed by superoxide dismutase (Eq. 5.6). H_2O_2 is then reduced to H_2O by ascorbate (AsA), a process that is catalyzed by ascorbate peroxidase (APX). AsA is oxidized to monodehydroascorbate radical, MDA (Eq. 5.7).

Additional electron pathways in chloroplasts that protect the photosynthetic apparatus from photo-oxidative stress are the Mehler reaction, xanthophyll cycle–dependent energy, the cyclic electron flow around PSI, the cyclic electron flow within PSII, and antioxidant metabolism (Mehler 1951; Heber et al. 1978; Verhoeven et al. 1997; Miyake and Yokota 2001; Miyake et al. 2002; Hirotsu et al. 2004). Nitrate assimilation is referred to as alternative electron flow (Makino et al. 2002). The Mehler reaction implies that the photoreduction of O_2 at PSI can produce superoxide radical $\left(O_2{}^{\bullet -}\right)$, which disproportionates to H_2O_2 (Mehler 1951; Asada 2006). It is estimated that the maximum rate of O_2 photoreduction is approximately 7.5 mmol $O_2{}^{\bullet -}\ (\text{mol Chl})^{-1}\ s^{-1}$ (30 mol (mg Chl)$^{-1}$ h^{-1}) in washed thylakoids, which corresponds to 5–10 % of the rate of total electron transport (Asada et al. 1974). It has also been observed that the $O_2{}^{\bullet -}$ reduction rate can reach a maximum around 2.0 kPa O_2 (Heber and French 1968; Takahashi and Asada 1982).

5.2 CO_2 Forms Used in Phytoplankton Photosynthesis

CO_2 and DIC (CO_2, H_2CO_3, $HCO_3{}^-$, and CO_3^{2-}) can be produced either photolytically or microbially from both DOM and POM (e.g. alage or phytoplankton) in natural waters (see also chapter "Photoinduced and Microbial Degradation of Dissolved Organic Matter in Natural Waters" and "Impacts of Global Warming on Biogeochemical Cycles in Natural Waters") (Jones 1992; Jansson et al. 2000; Meili et al. 2000; Grey et al. 2001; Hernes and Benner 2003; Tranvik et al. 2009; Ballaré et al. 2011; Zepp et al. 2011; Miller and Zepp 1995; Graneli et al. 1996; Granéli et al. 1998; Bertilsson and Tranvik 2000; Ma and Green 2004; Xie et al. 2004; Fu et al. 2007). This production varies seasonally and spatially depending on several factors such as contents of DOM and POM, solar intensity, water temperature and other geological and environmental conditions (White et al. 2010).

Gaseous CO_2 is rapidly dissolved in waters (Liu et al. 2010):

$$CO_2 + H_2O \leftrightarrow H_2CO_3 \leftrightarrow H^+ + HCO_3{}^- \leftrightarrow 2H^+ + CO_3^{2-} \tag{5.8}$$

where the reaction (Eq. 5.8) is an equilibrium mixture of dissolved carbon dioxide ($[CO_2]_{aq}$), carbonic acid (H_2CO_3), bicarbonate $\left(HCO_3{}^-\right)$ and carbonate $\left(CO_3{}^{2-}\right)$ ions with the pKa of 6.3 and 10.3 for $H_2CO_3 \leftrightarrow H^+ + HCO_3{}^-$ and $HCO_3{}^- \leftrightarrow H^+ + CO_3{}^{2-}$, respectively (Liu et al. 2010; Appelo and Postma

2005). The proportion of each species depends on pH: at high pH the reaction shifts to the right hand side of (Eq. 5.8) and HCO_3^- dominates at pH between 7 and 9, approximately 95 % of the carbon in water. At pH > 10.5, CO_3^{2-} predominates (Dreybrodt 1988). The equilibrium constants for this system are altered by the salinity of the medium: the values for seawater are an order of magnitude higher than those of freshwater toward the right-hand-side of the reaction (Raven et al. 2002; Millero and Roy 1997).

It is well known that the stable carbon isotope composition ($\delta^{13}C$ value) of organic matter, produced either by phytoplankton or terrestrial plants during photosynthesis, is significantly varied depending on the taxon-specific photosynthetic pathways (such as C_3, C_4, and crassulacean acid metabolism, CAM). It also varies depending on: variety of phytoplankton; diffusion of CO_2; incorporation of CO_2 by phosphoenolpyruvate carboxylase or Ribulose Bisphosphate Carboxylase-Oxygenase (Rubisco), and respiration; sources and interconversion of CO_2 and HCO_3^- (depending on a variety of environmental conditions including light intensity, temperature, DOM and POM contents, water depth, atmospheric CO_2 concentration and so on) (O'Leary 1981; Cooper and McRoy 1988; Farquhar et al. 1989; Raven and Farquhar 1990; Yoshioka 1997; Raven et al. 2002; Hu et al. 2012). Note that the $\delta^{13}C$ values of $[CO_2]_{aq}$ and DIC are −16.5 to −14.5 ‰ and −7.4 to −4.5 ‰, respectively (Yoshioka 1997). The values of $\delta^{13}C$ of organic matter in marine macroalgae and seagrass collected from the natural environment can vary from –2.7 ‰ to –35.3 ‰ (Raven et al. 2002; Hu et al. 2012; Beardall 2003; Hemminga and Mateo 1996; Raven 1997; Dunton 2001). Plants with C_4 characteristics show $\delta^{13}C$ values of −6 to −19 ‰ whilst plants with C_3 characteristics exhibit $\delta^{13}C$ values of −24 to −34 ‰ (Smith and Epstein 1971).

Such variation in the $\delta^{13}C$ value can be caused by (Farquhar et al. 1989; Raven and Farquhar 1990): (i) the isotope fractionation factor (α), which is the ratio of the reaction rates of $^{12}CO_2$ and $^{13}CO_2$ with Rubisco ($\alpha = 1.029$ for gaseous CO_2 and $\alpha = 1.030$ for dissolved CO_2); (ii) the relative contribution of phosphoenolpyruvate carboxylase (PEPC) activity to the photosynthetic carbon assimilation; and (iii) the supply of CO_2 to Rubisco is restricted by the boundary layer, stomata, and intercellular gas spaces that can differ for CO_2 diffusion in the gas phase ($\alpha = 1.0044$), and in the aqueous phase ($\alpha = 1.0007$).

The $\delta^{13}C$ values of POM are varied spatially and seasonally. They increase with increasing pH of lake water, which may reflect a shift by phytoplankton from using CO_2 to using HCO_3^- for photosynthesis (Zohary et al. 1994; Doi et al. 2006). The pH is increased with increasing water temperature during the time span of the summer stratification period, which may be connected with photoinduced degradation of DOM and POM (see also chapter "Photoinduced and Microbial Degradation of Dissolved Organic Matter in Natural Waters") (Kopáček et al. 2003; Mostofa et al. 2005). Photoinduced generation of H_2O_2 $\left(2O_2^{\bullet-} + 2H^+ \rightarrow H_2O_2 + O_2\right)$ (Mostofa and Sakugawa 2009; Fujiwara et al. 1993) might be one of the key factors for enhancing alkalinity or pH in waters. Therefore, uptake of HCO_3^- for phytoplankton photosynthesis at high pH might be the effect of its dominant presence in waters. A significant increase in the

δ^{13}C value in the phytoplankton bloom season suggests that phytoplankton photosynthesis may be limited by CO_2 depletion (Takahashi et al. 1990). It has been observed that aqueous CO_2, $[CO_2]_{aq}$, determined in freshwater and marine waters is relatively low (0.13–35 M) in freshwater and relatively higher (5–120 M) in seawater (Fogel et al. 1992; Francois et al. 1993; Yoshioka 1997; Takahashi et al. 1990; Herczeg and Fairbanks 1987). All aquatic phototrophs are depleted in δ^{13}C relative to dissolved inorganic carbon (DIC), because Rubisco discriminates against ^{13}C (Hu et al. 2012).

The spatial and temporal variability of δ^{13}C values in aquatic organisms depends on several factors such as isotopic shifts in available inorganic carbon, resulting from light-induced HCO_3^- utilization, variation in solar intensity, differences in water temperature, internal recycling of respiratory CO_2, photoinduced generation of DIC from DOM and POM, and dissolution of sedimentary carbonate (Yoshioka 1997; Raven et al. 2002; Jones 1992; Ma and Green 2004; Xie et al. 2004; White et al. 2010; Liu et al. 2010; Dreybrodt 1988; Hemminga and Mateo 1996; Campbell and Fourqurean 2009). It is shown that $[CO_2]_{aq}$ concentration is inversely correlated with the δ^{13}C of organic matter produced by phytoplankton (Rau et al. 1992; Freeman and Hayes 1992). The carbon isotope fractionation of phytoplankton could be a useful indicator for the assessment of its growth rate and of CO_2 availability (Fogel et al. 1992; Takahashi et al. 1991). Phytoplankton can actively transport CO_2 by a carbon-concentrating mechanism (CCM) that can affect its δ^{13}C value (Yoshioka 1997; Sharkey and Berry 1985; Bums and Beardall 1987; Thielmann et al. 1990). Correspondingly, ß-carboxylation catalysed by phosphoenolpyruvate carboxylase and phosphoenolpyruvate carboxykinase can affect the δ^{13}C of phytoplankton (Descolas-Gros and Fontugne 1985; Falkowski 1991).

To understand the mechanism behind the uptake of CO_2 or HCO_3^-, a fractionation equation was developed for plant photosynthesis (O'Leary 1981; Farquhar et al. 1989; Raven et al. 1993) and phytoplankton photosynthesis (Fogel et al. 1992; Rau et al. 1992; Francois et al. 1993; Jasper and Hayes 1994; Laws et al. 1995; Yoshioka 1997; Berry 1988).

5.2.1 Basic Equation for Expressing Photosynthetic Carbon Isotope Fractionation

The photosynthetic carbon isotope fractionation is initially derived based on the land C_3 plants (O'Leary 1981; Farquhar et al. 1989; Yoshioka 1997). The photosynthetic process for uptake of carbon can be depicted as follows (Yoshioka 1997)::

$$[CO_2]_{out} \underset{k_3}{\overset{k_1}{\longleftrightarrow}} [CO_2]_{in} \longrightarrow k_2 \text{ organic carbon} \tag{5.9}$$

where k_i is the rate constant for process i. Processes 1 and 3 are the diffusive influx and efflux of CO_2, respectively, whilst process 2 is the carboxylation step by

Rubisco. At steady state, or $d[CO_2]_{in}/dt = 0$, the overall fractionation factor (α) can be written as

$$\alpha = 1 + \Delta k_1 + (\Delta k_2 - \Delta k_1)\frac{Ci}{Ce} \tag{5.10}$$

where Ce and Ci are the CO_2 concentrations in air and at the carboxylation site, respectively, and $\Delta k_i = \alpha_i - 1$. In the equation (O'Leary 1981), subscripts for efflux and carboxylation steps are 2 and 3, respectively, and $E_i = 1 + \Delta k_i$:

$$\alpha = E_1(E_3/E_2 + k_3/k_2)(1 + \frac{k_3}{k_2}) \tag{5.11}$$

When $a = \Delta k_1$, $b = \Delta k_2$ and CO_2 concentrations in air and intercellular leaf spaces are denoted in partial pressure p_a and p_i, respectively, then (Eq. 5.10) can be modified into Farquhar's equation:

$$\Delta = \alpha - 1 = a + (b - a)\frac{p_i}{p_a} \tag{5.12}$$

On the other hand, the fractionation equation for passive diffusion-phytoplankton photosynthesis is substantially similar to that of land C_3 plants (Eq. 5.10). The CO_2 diffusion must be considered in the aqueous phase and Ce denotes the CO_2 concentration in bulk solution or $[CO_2]_{aq}$. The term 'CO_2 demand' = 'Ce – Ci' has been introduced into the new model (Rau et al. 1992). The relationship between the $\delta^{13}C$ value of POM and $[CO_2]_{aq}$ can be determined using the fractionation equation that includes the (Ce–Ci) term:

$$\varepsilon_p = \varepsilon_1 + \left(1 - \frac{Ce - Ci}{Ce}\right)(\varepsilon_2 - \varepsilon_1) \tag{5.13}$$

where (Ce – Ci) = 7–8 μM in southwestern Indian Ocean. When (Ce – Ci) is constant, the (Eq. 5.10) at infinite Ce can be expressed as:

$$\alpha = 1 + \Delta k_2 \tag{5.14}$$

This implies that the overall fractionation can reach a maximum value, which corresponds to that of Rubisco (α = 1.027–1.029, or Δk_2 = 0.027 – 0.029) at high Ce (Roeske and O'Leary 1984; Farquhar and Richards 1984). Furthermore, (Ce – Ci) may increase with increasing Ce as found in a culture study of *Skeletonema costatum* and *Emiliania huxley*, which introduces the possibility of β-carboxylation at high Ce (Hinga et al. 1994). Interestingly, the activity of the PEPCKase of *S.costatum* can increase to >50 % of Rubisco activity at the end of growth (Descolas-Gros and Fontugne 1985, 1990).

The low fractionation observed at high Ce is possibly due to β-carboxylation (Goericke and Fry 1994), particularly in the case of PEPCKase-mediating β-carboxylation. The latter shows similar discrimination against $^{13}CO_2$ as that of Rubisco (Arnelle and O'Leary 1992). Active transport by CCM may contribute to a fractionation at high Ce, which is lower than that given by the fractionation equation (Yoshioka 1997). It is shown that passive CO_2 diffusion is efficient to sustain maximum growth of *Phaeodactylum tricornutum*, which does not require active transport of inorganic carbon at $[CO_2]_{aq} = 10$ M (Laws et al. 1995). This study also shows that maximum growth rate is expected when the CO_2 influx is equal to the growth rate (Laws et al. 1995). In that case, Ci = 0 and also the growth rate (photosynthetic activity) is zero or even negative, because of the oxygenase activity of Rubisco (Yoshioka 1997). The contradiction may occur because the growth rate is not independent of Ce and Ci. Therefore, diffusive transport of CO_2 can operate together with active transport (Yoshioka 1997), and CCM possibly requires an energy expenditure (Berry 1988). However, it is difficult to identify the relative contribution of active transport to the total CO_2 influx from the ealier fractionation equations. In the derivation of (Eq. 5.10), it is assumed that the resistance to CO_2 diffusion is similar in either direction across the cell membrane, or $k_1 = k_3$ (Francois et al. 1993). This assumption originally came from the expectation that resistance to CO_2 diffusion through the stoma of a plant leaf would be the same in both directions (O'Leary 1981). Aquatic phytoplankton may have a CCM with different values for this resistance ($k_1 \neq k_3$), probably ($k_1 > k_3$), and thus the fractionation equation can be rewritten as:

$$\alpha = 1 + \Delta k_1 + (\Delta k_2 - \Delta k_1)\frac{k_3\mathrm{Ci}}{k_1\mathrm{Ce}} \tag{5.15}$$

which may provide some measure of the contribution of active transport. It is generally assumed that the resistances to CO_2 diffusion in both directions across the cell membrane are the same (symmetric permeability). A fractionation equation is required to express the decrease in fractionation with increasing contribution of active transport (*f*), as some function *f* (Yoshioka 1997). Basically, *f* and $k_1 \neq k_3$ may have the same importance for CO_2 acquisition by phytoplankton. Therefore, active transport of inorganic carbon by CCM may be linked (as a homologue) to the asymmetric permeability of the cell membrane for CO_2.

Deviation of Fractionation Equations Involving Active Transport (*Yoshioka 1997*)

Various phytoplankton species can actively transport CO_2 and HCO_3^- in aqueous media (Bums and Beardall 1987). However, they depend on two phenomena: (i) the occurrence of internal and external carbonic anhydrase (CA), which can catalyse the equilibrium between CO_2 and HCO_3^- and can affect the determination of the inorganic carbon species crossing the cell membrane; (ii) the difference in inorganic carbon species can substantially vary the fractionation factor of the substrate for photosynthesis. It is shown that fractionation between $[CO_2]_{aq}$ and HCO_3^- can differ by at most 10 ‰ in both equilibrium- and CA-catalyzed reactions (Deines et al. 1974; Paneth and O'Leary 1985). Considering these phenomena, it is important to develop the fractionation equations for two cases in which transported carbon has the δ^{13}C value of either bulk $[CO_2]_{aq}$ or HCO_3^-.

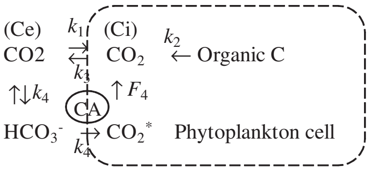


Fig. 8 Schematic presentation of the active transport of CO_2. The $\delta^{13}C$ of the actively transported carbon (CO_2^*) is assumed to be the same as that of the CO_2 in the medium (Ce). *Data source* Yoshioka (1997)

(1) ***Active transport of CO_2***. The $\delta^{13}C$ value of actively transported inorganic carbon is assumed to be the same as that of Ce (Fig. 8). Extracellular CA may contribute to the conversion of HCO_3^- to CO_2 at the cell surface.

At steady state:

$$\frac{\mathrm{dCi}}{\mathrm{d}t} = k_1\mathrm{Ce} + F_4 - (k_2 - k_3)\mathrm{Ci} = 0 \tag{5.16}$$

where F_4 is the is the flux of actively transported CO_2.
The relative contribution of active transport (f) can be defined by:

$$f = \frac{F_4}{k_1\mathrm{Ce} + F_4} \tag{5.17}$$

If $0 \leq f < 1$, (Eq. 5.17) can be rewritten as:

$$\frac{\mathrm{dCi}}{\mathrm{d}t} = \frac{1}{1-f}k_1\mathrm{Ce} - (k_2 + k_3)\mathrm{Ci} = 0 \tag{5.18}$$

Overall, fractionation becomes:

$$\alpha = 1 + \Delta k_1 + (\Delta k_2 - \Delta k_1)(1 - f)\frac{\mathrm{Ci}}{\mathrm{Ce}} \tag{5.19}$$

By assuming the same f value for $^{12}CO_2$ and $^{13}CO_2$, and $\Delta k_1 = \Delta k_3$, (Eq. 5.19) becomes the same as (Eq. 5.15) when k_1/k_3 is substituted for $(1 - f)$. This supports the expectation that active transport might be linked with the asymmetric permeability of the cell membrane for CO_2. Leakiness, X (the ratio of efflux to influx of DIC) (Berry 1988), can be expressed as follows:

$$X = 1 + \frac{k_3\mathrm{Ci}}{k_1\mathrm{Ce}\,\mathrm{F}_4}(1 - f)\frac{\mathrm{Ci}}{\mathrm{Ce}} \tag{5.20}$$

When all carbon is transported by active transport ($f = 1$), k_1Ce would be zero. In that case, one cannot substitute $f = 1$ in (Eq. 5.19), because the denominator in (Eq. 5.18) becomes zero. Then, α becomes:

X is not zero, but

$$\begin{aligned}\alpha &= 1 + \frac{\Delta k_2 - \Delta k_1}{\Delta k_1 + 1}\frac{k_3\mathrm{Ci}}{\mathrm{F}_4} \\ &= 1 + (\Delta k_2 - \Delta k_1)\frac{k_3\mathrm{Ci}}{\mathrm{F}_4}\end{aligned} \tag{5.21}$$

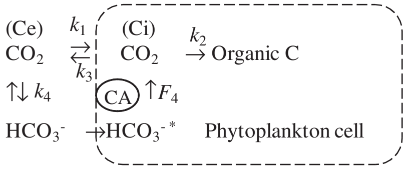


Fig. 9 Schematic presentation of the active transport of HCO_3^-. The $\delta^{13}C$ of the actively transported carbon (HCO_3^{-*}) is assumed to be the same as that of HCO_3^- in the medium. *Data source* Yoshioka (1997)

$$X = \frac{k_3 \mathrm{Ci}}{F_4} \tag{5.25}$$

(2) ***Active transport of HCO_3^-***: The transported carbon has the same $\delta^{13}C$ value as HCO_3^-, as depicted in the scheme shown in (Fig. 9). The overall fractionation equation is substantially different from Eq. (5.19), although the steady-state for Ci is denoted by a similar term as Eq. (5.16), which can be written as:

$$\alpha = \frac{(\Delta k_1 + 1)(\Delta k_3 + 1)(1 - X) + (\Delta k_1 + 1)(\Delta k_2 + 1)X}{(\Delta k_3 + 1)(1 - f) + (\Delta k_1 + 1)(\Delta k_3 + 1)(\Delta k_4 + 1)f} \tag{5.23}$$

where Δk_4 denotes the fractionation in the CO_2—HCO_3^- dissociation process. Note that f and X are the same as those in the active transport of CO_2.

Considering that the second- and third-order terms of Δk_i are negligible, and $\Delta k_1 = \Delta k_3$, then α can be approximated as follows:

$$\alpha = 1 + \Delta k_1(1 - f) + (\Delta k_2 - \Delta k_1)(1 - f)\frac{\mathrm{Ci}}{\mathrm{Ce}} - \Delta k_{4f} \tag{5.24}$$

When $f = 1$, α becomes:

$$\alpha = 1 + (\Delta k_2 - \Delta k_1)\frac{k_3 \mathrm{Ci}}{F_4} - \Delta k_4 \tag{5.25}$$

which implies that the overall fractionation decreases by ($\Delta k_1 + \Delta k_4$) when all carbon derives from the active transport of HCO_3^- $(f = 1)$, compared to the passive diffusion model (Eq. 5.15). It can be deduced from (Eq. 5.24) that all fractionation steps, including overall fractionation would be affected by f. The difference between (Eqs. 5.19 and 5.24) or ($\Delta k_1 + \Delta k_4$) corresponds to the difference in $\delta^{13}C$ values between CO_2 and HCO_3^-. These equations indicate that the overall fractionation from $[CO_2]_{aq}$ to organic carbon may be less than unity under some conditions (Yoshioka 1997).

From a reanalysis of Hinga's data (Hinga et al. 1994) one gets that the active transport of CO_2 for *S. costatum* can contribute ~ 30–40 % of the total carbon influx. The relative contribution of active transport can reach 25–35 %, without any change in CO_2 demand for an uptake of 10 % of the total carbon mediated by β-carboxylation

(Yoshioka 1997). Finally, carbon assimilation by various kinds of phytoplankton, such as *S. costatum*, *Microcystis* spp. and others (Fogel et al. 1992; Francois et al. 1993; Yoshioka 1997; Takahashi et al. 1990; Herczeg and Fairbanks 1987; Hinga et al. 1994) may operate under almost constant CO_2 demand, amounting on average to 4.4 μM in seawater and 0.29 μM in freshwater (Yoshioka 1997). Phytoplankton photosynthesis is largely dependent on habitats (either seawater or freshwater), and on phytoplankton species that have variable efficiency for CCM. The process involves either active transport of HCO_3^-, or coupled dehydration of HCO_3^- by a cell-surface carbonic anhydrase and CO_2 transport (MacIntyre et al. 2000; Badger and Price 1992; Tortell et al. 1997; Berman-Frank et al. 1998; Nimer et al. 1999).

5.3 Variation in Temperature

Temperature, driven by solar radiation, is one of the key factors for variating the primary production by photosynthesis in natural waters (Sobek et al. 2007; Mortain-Bertrand et al. 1988; Davison 1991; Wilen et al. 1995; Lesser and Gorbunov 2001; Baulch et al. 2005; Doyle et al. 2005; Yoshiyama and Sharp 2006; Ogweno et al. 2008; Bouman et al. 2010; Fu et al. 2007). This effect can be discussed, based on aquatic microorganisms and higher plants.

Temperature Effects on Aquatic Microorganisms

Cyanobacteria, the most ancient life forms on earth, are unusual prokaryotic microorganisms that are able to perform oxygenic photosynthesis. Optimum growth, with respect to optimal temperatures, is in this case influenced by their ability to tolerate temperature stress, such extreme cold in Antarctica (where temperatures never exceed −20 °C) and in water pockets of Antarctic lake ice, where temperatures are always below 0 °C. At the opposite end of the variation scale there are extremely high temperatures such as 55–60 °C and even the case of hot springs, where temperatures reach 70 °C (Schopf et al. 1965; Meeks and Castenholz 1971; Margulis 1975; Priscu et al. 1998; Psenner and Sattler 1998; Ward et al. 1998).

At ambient water temperature (WT), the primary excitation requires 2–3 ps, and the subsequent electron transfer to the primary quinone QA exhibits multiphasic kinetics (80–300 ps) (Dashdorj et al. 2004). It is commonly considered that that the primary excitation occurs within 1–3 ps after the creation of the electronically excited special pair P700* (Brettel 1997; Dashdorj et al. 2004). The state of thylakoid membranes in cyanobacteria plays a prominent role in the tolerance of the photosynthetic machinery to environmental stresses, such as cold (chilling) (Wada et al. 1990; Murata et al. 1992).

At low temperatures, ultrafast time-resolved spectroscopy suggests multiexponential evolution of the excited state and of photoproduct populations, even when excitation takes place in the red edge of the absorption spectrum (Germano et al. 2004). The different time components observed at low temperatures are generally recognized to produce charge separation. The latter can either take place through direct excitation of the primary donor by 1–5 ps (Prokhorenko and Holzwarth 2000; Tang et al. 1990; Germano M et al. 1995; Groot et al. 1997; Konermann et al. 1997; Greenfield et al. 1999), or be slowed down by energy transfer to the primary donor in tens or hundreds of picoseconds (Groot et al. 1997; Greenfield et al. 1999). However, calculations based on structural information, from both the crystallographic structure and a model, predict subpicosecond excitation energy equilibration among the six central cofactors (Durrant et al. 1995; Renger and Marcus 2002; Zouni et al. 2001; Kamiya and Shen 2003; Svensson et al. 1996; Leegwater et al. 1997). Electron transfer thus occurs from other Chls, and the slower components observed in the tens of picoseconds timescale at low temperatures are due to secondary electron transfer (Prokhorenko and Holzwarth 2000). A model study has shown that the ~67 % variability of observed primary production indicates that estuarine production is mainly controlled by light availability and temperature (Yoshiyama and Sharp 2006). Bacterial abundance (12×10^6 mL^{-1}) and production (1.7 g C L^{-1} h^{-1}) depend on temperature. During late spring and summer, at constantly higher temperatures, bacterial production can correlate positively with readily utilisable substrates and humic compounds (Freese et al. 2007).

High surface temperatures and heavy precipitation in late spring and summer can give rise to a highly-stratified water column that can stimulate a series of phytoplankton blooms. During winter in Tokyo bay, a weakly-stratified and deeply-mixed water column can lead to a rapid decline in phytoplankton biomass under light-limited growth conditions (Bouman et al. 2010). The effect of high WT can be a decrease in PSII efficiency, which can ultimately cause cell stress (Lesser and Gorbunov 2001).

At highly elevated WT, several effects on phytoplankton can take place such as disorganization of thylakoid membranes, disrupted electron flow to the dark reactions of photosystem II, elevated concentrations of damaging oxygen and hydroxyl radicals, and the loss of the D1 repair protein (Goulet et al. 2005). The mechanism behind the changes in photosynthetic efficiency caused by WT, driven by natural solar intensity, mostly follows a similar mechanism as sunlight effects (see the earlier section). However, WT can cause photosynthetic efficiency to be either enhanced or decreased, an issue that involves three facts: First, at low WT (lower than 12 °C, including chilling stress that generally refers to nonfreezing temperatures at 0–12 °C) the key reactants such as CO_2, H_2O_2 and DIC (generated both photolytically and microbially from DOM and POM) are quite low at low sunshine in natural surface waters. Low availability of these reactants can decrease the photosynthetic efficiency of aquatic microorganisms in natural waters.

Second, at moderate WT (approximately 12–25 °C) and with an increase in WT, the key reactants are significantly increased, usually also because of enhanced sunlight intensity. This effect may greatly enhance photosynthesis at optimum WT and, as a consequence, primary production in waters. It has been shown that the Chl *a* concentrations at the epilimnion are well correlated with WT in lakes, but those correlations are not observed in the deeper layers (Fu et al. 2010; Mostofa KMG et al., unpublished data). This suggests that an optimum water temperature, driven by solar intensity, may play a significant role in the origin of Chl *a* or in enhancing phytoplankton biomass in natural waters.

At highly elevated WT (approximately >25–50 °C), photoinduced and microbial degradation of DOM and POM is extremely enhanced, with extremely high generation of H_2O_2, CO_2 and DIC. It has been shown that $[CO_2]_{aq}$ is significantly higher (~10–120 M) at 25 °C than at 15 °C (~5–110 M) or at 9 °C (~5–50 M) in marine waters (Hinga et al. 1994). This effect can cause extremely high photosynthesis and high primary production. This can be supported by the synergistic effect of high H_2O_2, combined with high seawater temperature, which can cause a 134 % increase in respiration rates. Such an increase surpassed the effect of either H_2O_2 or high seawater temperature alone (Higuchi et al. 2009). High temperature, driven by strong solar intensity, is responsible for high production of H_2O_2 (see also chapter "Photoinduced and Microbial Generation of Hydrogen Peroxide and Organic Peroxides in Natural Waters") (Mostofa and Sakugawa 2009), which is directly linked with photosynthesis. Simultaneously, this process can also generate a high amount of ROS such as $O_2^{\bullet-}$, $^1O_2$, H_2O_2, and $HO^{\bullet}$. The latter is a strong oxidizing agent, produced either from H_2O_2 (via direct photo-dissociation by sunlight or photo-Fenton reaction) or other sources, such as the direct photolysis of NO_2^- and NO_3^- (see the chapters "Photoinduced and Microbial Generation of Hydrogen Peroxide and Organic Peroxides in Natural Waters", "Photoinduced Generation of Hydroxyl Radical in Natural Waters" and "Photoinduced and Microbial Degradation of Dissolved Organic Matter in Natural Waters"). This effect can significantly degrade algal or phytoplankton cells, thereby decreasing the photosynthetic efficiency. All these processes should be able to significantly promote the photosynthetic efficiency in waters with high contents of DOM and POM.

Temperature Effects on Higher Plants

Plants need an optimum temperature for photosynthesis. The stress represented by extremely high- or low-temperature has a significantly negative effect on the growth and productivity of plants (Allen and Ort 2001; Adams et al. 2002; Adams Iii et al. 2004; Öquist and Huner 2003; Yang et al. 2009). It has been shown that suboptimal and above-optimal temperatures can promote photoinhibition, caused by an over-excitation of photosystems (Powles 1984; Öquist et al. 1993; Huner et al. 1998). Effects of temperature on the photosynthesis of plants have been discussed as follows: First, low temperature stress or chilling stress (generally at 0–12 °C) can highly inhibit growth and development of most plants, and in particular of those coming from tropical and subtropical regions (Allen and Ort 2001; Yang et al. 2009; D'Ambrosio et al. 2006).

The chilling stress or lower temperatures can affect several physiological functions and induce water deficiency. Commonly observed effects are decrease of leaf water potential, of electron transport rate, of total Chl contents, of CO_2 uptake and of the carotenoid content; stomatal closure; inhibition of thylakoid electron transport and photophosphorylation; Rubisco inactivation; inhibition of carbohydrate metabolism; and finally, a significant decrease of the maximum quantum efficiency of PSI and PSII primary photochemistry (Allen and Ort 2001; Yang et al. 2009; D'Ambrosio et al. 2006; Berry and Bjorkman 1980; Eamus 1986; Sage and

Sharkey 1987; Huner et al. 1993; Ebrahim et al. 1998; Sundar and Ramachandra Reddy 2001; Caramori et al. 2002; Kudoh and Sonoike 2002; Yu et al. 2002; Huang and Guo 2005). The latter effect can limit the photosynthetic rates or processes of chilling-sensitive plants.

It is also shown that low temperatures can inhibit the enzymes of carbon assimilation, such as fructose-1,6-bisphosphatase and sedoheptulose-1,7-bisphosphatase (D'Ambrosio et al. 2006; Sassenrath et al. 1990; Sassenrath and Ort 1990). It has also been shown that the O_2-induced inhibition of photosynthesis can increase with temperature, from 12.2 % at 5 °C to 33.5 % at 35 °C (D'Ambrosio et al. 2006). Plants of *B. vulgaris* exposed to low temperatures (5–15 °C) also show a significant stimulation of CO_2 assimilation at 2 % O_2 concentration (D'Ambrosio et al. 2006). The inhibition of photosynthesis (photorespiration) at high temperatures is generally caused by the increase of the ratio oxygenase/carboxylase activity of Rubisco (Sage and Sharkey 1987).

It has been observed that low night temperature under chilling conditions (mostly affected at 5 °C) can increase photoinhibition of photosynthesis with a marked loss of D1 and 33 kDa proteins in various plants (Yang et al. 2009; Sundar and Ramachandra Reddy 2001; Lidon et al. 2001; Bertamini et al. 2006). This can be due to accumulation of soluble sugars and reduced orthophosphate cycling from the cytosol back to the chloroplast. Therefore, it limits the ATP synthesis needed for Rubisco regeneration (Ebrahim et al. 1998; Hurry et al. 1998). Inhibition of photosynthetic electron transport is susceptible to lessen net photosynthesis in some chilling-sensitive plant species, despite relatively minimal reductions in the ratio of variable to maximum chlorophyll (Chl) fluorescence (F_v/F_m). Such an effect is due to the net photoinactivation of PSI rather than PSII (Bertamini et al. 2006; Tjus et al. 1998; Sonoike 1999). A significant decrease of electron transport rate under chilling conditions might cause a low temperature-induced limitation of carbon metabolism. Furthermore, sinks of electrons can result in alternative processes to CO_2 fixation (D'Ambrosio et al. 2006; Huner et al. 1993; Osmond 1981; Hendrickson et al. 2003, 2004). The decrease of electron transport in PSII (D'Ambrosio et al. 2006) is susceptible to decrease in the photoinduced generation of $O_2^{\bullet-}$ and then H_2O_2, which is directly liked to the occurrences of photosynthesis. The decrease in the contents of H_2O_2 production at chilling conditions can decrease the photosynthesis that subsequently decreases the growth and development of plants. This effect is mostly responsible for other physiological changes in plants at chilling stress.

It has also been observed that a significant increase of the proportion of electron flow in chilling conditions can occur in non-assimilative processes in some plants, such as maize and grapevine leaves (Fryer et al. 1998; Flexas et al. 1999). These studies suggest that a higher electron flow could reach O_2, by the Mehler reaction, as an alternative acceptor to CO_2 at low temperatures. This effect can enhance the production of ROS such as $O_2^{\bullet-}$ and H_2O_2, which may not be used in photosynthesis because of CO_2 shortage and other still unknown reasons. In contrast, H_2O_2 and photogenerated $HO^{\bullet}$ can damage the cells. Coherently, damage of chlorophyll-protein complexes and pigments in has been observed in plant cells under chilling condition (Powles 1984; Kudoh and Sonoike 2002; Bongi and Long 1987; Garstka et al. 2007). The decrease of the carotenoid content at lower temperatures in *B. vulgaris* can enhance damage by ROS, because of the important photoprotective function of carotenoids in scavenging highly destructive singlet oxygen. Furthermore, they can prevent $^1O_2$ formation by reacting with the chlorophyll triplet state (Havaux et al. 1998). Low temperature stress can also enhance photodamage to PS II under strong light (Wada et al. 1990; Murata et al. 1992; Öquist et al. 1993; Öquist and Huner 1991), and repair of PS II under low-temperature stress conditions is inhibited both in *Synechocystis* and plants (Gombos et al. 1994; Wada et al. 1994; Moon et al. 1995; Alia et al. 1998).

At higher temperature (>25 °C) caused by heat stress or drought stress, photosynthetic efficiency is significantly altered and can lead to decreased growth and development of plants (D'Ambrosio et al. 2006; Pastenes and Horton 1996; Pastenes and Horton 1996; Salvucci and Crafts-Brandner 2004; Sharkey 2005). The effect of high temperature on organisms is expected to become more and more significant. The global mean temperature has increased by 0.6 °C from 1990 to 2000 and is projected to increase by another 1.4 to over 5 °C by 2100 (see chapter "Impacts of Global Warming on Biogeochemical Cycles in Natural Waters" for detailed description). Heat stress can induce several processes such as: saturation of electron transport rate and disruption of its activity; decrease of stomatal conductance; increase in increase in O_2-consuming photorespiration and non-photoinduced quenching; decreased affinity of the enzyme for CO_2; decrease in CO_2 fixation; inactivation of the oxygen-evolving enzymes of PSII; increase in the activity of antioxidant enzymes such as superoxide dismutase, ascorbate peroxidase, guaiacol peroxidase, and catalase; decrease in PSII activity, and finally of photosynthetic capacity (Ogweno et al. 2008; D'Ambrosio et al. 2006; Pastenes and Horton 1996; Pastenes and Horton 1996; Salvucci and Crafts-Brandner 2004; Sharkey 2005; Schuster and Monson 1990; Heckathorn et al. 2002; Mazorra et al. 2002; Barua et al. 2003; Núñez et al. 2003; El-Shintinawy et al. 2004; Rivero et al. 2004; Cao et al. 2005).

Moderate heat stress can cause increased thylakoid proton conductance and increased cyclic electron flow around PSI (Pastenes and Horton 1996; Bukhov et al. 1999, 2000; Bukhov and Carpentier 2000; Egorova and Bukhov 2002). PSI-mediated cyclic electron flow can occur via either of two routes: the first is antimycin A-sensitive and involves ferredoxin plastoquinone reductase; the second one involves the NAD(P)H dehydrogenase complex (Bukhov et al. 2000; Thomas et al. 1986; Boucher et al. 1990; Joët et al. 2001).

It has also been shown that high temperatures stress (often above 45 °C) can damage PSII (Terzaghi et al. 1989; Thompson et al. 1989; Gombos et al. 1994; Çjánek et al. 1998; Yamane et al. 1998). Furthermore, photorespiration increases with increasing temperature, faster than photosynthesis (Schuster and Monson 1990). High leaf temperatures can reduce plant growth, and it is estimated that up to 17 % decrease in crop yield can occur for each degree Celsius increase of average temperature during the growing season (Lobell and Asner 2003). Additionally, leaves with low transpiration rates (e.g. oak leaves) can suffer frequent high-temperature episodes when leaf temperature can exceed the air temperature by as much as 15 °C (Singsaas and Sharkey 1998; Hanson et al. 1999; Singsaas et al. 1999). Rubisco can produce hydrogen peroxide as a result of oxygenase side reactions, which can increase substantially with temperature (Sharkey 2005).

Moreover, an increase in temperature can induce sinks of electron transport different from CO_2 assimilation, and photorespiration is increased at 30–35 °C (D'Ambrosio et al. 2006). The O_2-independent electron transport can account for up to 20 % of the total PSII electron transport in wild watermelon leaves (Miyake and Yokota 2000, 2001). The electron flux in PSII that exceeds the flux required for the cycles of photosynthetic carbon reduction and photorespiratory carbon oxidation, can induce photoreduction of O_2 in the water–water cycle (Miyake and Yokota 2000, 2001). It has been shown that the greater partitioning of reductive power to non-assimilative processes consuming O_2 (photorespiration, Mehler reaction and chlororespiration) with respect to CO_2 assimilation allows keeping the PSII efficiency factor unmodified at temperatures as high as 35 °C (D'Ambrosio et al. 2006).

The unsaturation of fatty acids can protect PSII from the inhibition of the activity that is caused by strong light at low temperatures (Wada et al. 1990; Murata et al. 1992), and can accelerate the repair of photodamaged PSII (Gombos et al. 1994; Wada et al. 1994; Moon et al. 1995). After photodamage to PSII in *Synechocystis* at low temperatures (0–10 °C), activity recovery can reach up to 50 % of the original level in the darkness at moderate temperatures, without the de novo synthesis of D1 protein (Nishiyama et al. 2008).

High-temperature stress can disrupt the cellular metabolic homeostasis and promote the production of reactive oxygen species (H_2O_2, $^1O_2$, $O_2^{\bullet -}$, and $HO^{\bullet}$) (Mittler 2002). Oxidative stress occurs in any plant cell when there is an imbalance between production of ROS and antioxidant defense (Apel and Hirt 2004; Mittler 2002; Scandalios 2002). The consequence is a decrease of the net photosynthetic efficiency that affects various plant activities (Ogweno et al. 2008; Apel and Hirt 2004; García-Ferris and Moreno 1994; Alscher et al. 1997; Anderson 2002; Irihimovitch and Shapira 2000; Pfannschmidt 2003). Calvin-cycle enzymes within chloroplasts are particularly sensitive to high levels of H_2O_2, which decreases CO_2 fixation and foliar biomass (Willekens et al. 1997; Zhou et al. 2004, 2006). The mechanism behind the decline of plant photosynthesis by high-temperature stress, driven by high irradiance or drought or heat stress, is similar to that of high irradiance as mentioned earlier.

5.4 *Effects of Water Stress (Drought) and of Precipitation/Rainfall*

Water stress or drought stress can significantly affect plant photosynthesis and decrease their growth, development and productivity (Li and van Staden 1998; Hassan 2006; Liu et al. 2006; Ohashi et al. 2006; Fariduddin et al. 2009). Water or drought stress can stimulate changes in water balance, leaf area expansion, absorption of photosynthetically active radiation, stomatal closure that reduces the internal CO_2 concentration, integrity of membranes and proteins, metabolic dysfunction, damage at the cellular and subcellular membrane levels via lipid peroxidation, loss of activity of membrane-based enzymes, chloroplast capacity, and PSII activities (Jones and Turner 1978; Matsuda and Riazi 1981; Kaiser 1987; Asada 1992; Hopkins and Hüner 1995; Aziz and Larher 1998; Nam et al. 1998; Cornic 2000; Wilson et al. 2000; Lawlor 2002; Velikova and Tsonev 2003; Flexas et al. 2004; Hassan 2006; Fariduddin et al. 2009; Munns et al. 1979). The final result is a decline in net photosynthesis. The drought stress can reduce stomatal conductance and lead to decreased carbon assimilation, with consequently low biomass production (Fariduddin et al. 2009; Medrano et al. 2002). Decrease in photosynthetic efficiency is generally attributed to reduced CO_2 supply resulting from stomatal closure (Hsiao 1973). A decrease in nitrate reductase activity can inhibit protein synthesis, inactivate enzymes, and reduce the flux of nitrate to the leaf (Fariduddin et al. 2009; Morilla et al. 1973; Shaner and Boyer 1976). The rapid loss of nitrate reductase activity could be part of a biochemical adaptation to water deficit, shutting off the nitrate assimilation pathway and preventing accumulation of nitrite and ammonium (Huffaker et al. 1970).

Cell membranes, which are structurally composed of large amounts of polyunsaturated fatty acid, are highly susceptible to react photolytically with possible changes in membrane fluidity, permeability, and cellular metabolic functions (Bandyopadhyay et al. 1999). The elevation in the antioxidant system defences can detoxify the reactive oxygen species generated by drought stress and can thereby recover the altered physiological performance of stressed plants (Fariduddin et al. 2009).

Water (drought) stress and high temperature together can cause a marked decrease of PSII activity that, together with other functions, can lead to a significant decrease in the net photosynthetic rate of plants (Hassan 2006; Flagella et al. 1998; Hassan et al. 1998; Yordanov et al. 1997, 1999, 2000). It has been shown that this effect may be caused by stomatal and non-stomatal limitations. Stomatal closure usually occurs before inhibition of photosynthesis and restricts CO_2 availability at the assimilation sites in chloroplast. In contrast, non-stomatal limitation of photosynthesis has been attributed to reduced carboxylation efficiency, reduced ribulose-1,5-bisphosphate (RuBP) regeneration, or inhibited chloroplast activity (Wise et al. 1992; Lawlor 1995; Shangguan et al. 1999). Conversely, water stress mostly causes a progressive suppression of photosynthetic carbon assimilation in desiccation-tolerant and intolerant wheat plants (Deltoro et al. 1998).

The mechanism behind the water (drought) stress effect of decreasing photosynthesis is similar to that of high-irradiance/high temperature stress. It occurs particularly in tropical and subtropical regions as mentioned before. Moreover, water stress or drought in low temperature regions can decrease the water content of plant cells that contain dissolved O_2. Shortage of dissolved O_2 in response to water stress can decrease the photoinduced generation of H_2O_2, which is directly linked to photosynthesis. This effect can decrease photosynthesis and cause decline in growth or death of organisms.

The water stress can shift the temperature threshold towards higher values and cause an increase of the heat resistance (Yordanov et al. 1997, 2000; Havaux

1992). Some desiccation-tolerant cells accumulate large amounts of the disaccharides trehalose and/or sucrose. Of these, mostly trehalose can prevent damage from dehydration, not only by inhibiting fusion between adjacent membrane vesicles during drying, but also by maintaining membrane lipids in the fluid phase in the absence of water (Singh et al. 2002; Crowe et al. 1987, 1992; Leslie et al. 1994). Trehalose can depress the phase transition temperature of the dry lipids after desiccation and maintain them in the liquid crystal state (Crowe et al. 1992; Leslie et al. 1994). The increasing activities of catalase, peroxidase and superoxide dismutase and the level of proline can constitute a natural endogenous defense system that increases the response to water stress (Fariduddin et al. 2009; Schützendübel and Polle 2002).

Rainfall can greatly increase photosynthesis, particularly by increasing various physiological phenomena such as leaf water potential, net photosynthetic rate, stomatal conductance, and transpiration (Souch and Stephens 1998; Smit and Rethman 2000; Morris et al. 2004; Li et al. 2007). Moreover, it can significantly enhance the sudden growth of plants all over the world at the beginning of summer season and at the end of winter season. The consequence is an increase of annual biomass production and a simultaneous increase of the production of various food and crops. Maximum photoinduced efficiency of PSII is significantly increased with an increase in rainfall (Li et al. 2007). Among other issues, this might also be caused by the occurrence of H_2O_2 and nutrients in rain water. The supply of exogenous H_2O_2 from rainfall (up to 200 μM, see chapter "Photoinduced and Microbial Generation of Hydrogen Peroxide and Organic Peroxides in Natural Waters") could enhance photosynthesis and make PSII reach its maximum photoinduced efficiency. On the other hand, leaf wetness causes not only instantaneous suppression of photosynthesis but also chronic damage to the photosynthetic apparatus (Ishibashi and Terashima 1995). Interestingly, a direct link has been observed between rainwater H_2O_2 content and the rate of photosynthesis (Komissarov 1995, 2003; Mostofa et al. 2009). However, high concentrations of H_2O_2 (50–100 M) in the presence of iron (Fe) and oxalate can generate $HO^\bullet$ that would decrease plant productivity and growth (Kobayashi et al. 2002).

In the case of aquatic microorganisms, drought stress or absence of rainfall for a longer period can significantly affect photosynthesis. In this case, similar mechanisms are followed as for high light irradiance as explained in the earlier section.

5.5 Effects of the Contents and Nature of DOM and POM

Organic matter (OM) consisting of DOM and POM is one of the key factors that can produce nutrients (NO_2^-, NO_3^- and PO_4^{3-}) and various photo- and microbial products, such as H_2O_2, CO_2, DIC, LMW DOM, and so on (see also chapters "Dissolved Organic Matter in Natural Waters", "Photoinduced and Microbial Degradation of Dissolved Organic Matter in Natural Waters", "Chlorophylls and Their Degradation in Nature", and "Impacts of Global Warming on

Biogeochemical Cycles in Natural Waters") (Mostofa et al. 2009; Mostofa and Sakugawa 2009; Zhang et al. 2009; Tranvik et al. 2009; Zepp et al. 1987, 2011; Mostofa et al. 2011; Graneli et al. 1996; Granéli et al. 1998; Ma and Green 2004; White et al. 2010; Liu et al. 2010; Fu et al. 2010; Palenik et al. 1987; Cooper and Lean 1992; Bushaw et al. 1996; Molot et al. 2005; Kim et al. 2006; Johannessen et al. 2007; Borges et al. 2008; Li et al. 2008; Kujawinski et al. 2009; Lohrenz et al. 2010; Omar et al. 2010; Cai 2011). Such processes can influence photosynthesis directly or indirectly in water.

Photoinduced degradation of DOM and POM (POM includes e.g. phytoplankton) can be summarized as follows (Eq. 5.29):

$$\begin{aligned}&\mathrm{DOM + POM + h\upsilon \rightarrow\ H_2O_2 + CO_2 + DIC +\ LOW\ DOM +\ NO_3{}^- + NO_2{}^-}\\&\mathrm{+PO_4^{3-} + autochthonous\ DOM +\ other\ species}\end{aligned} \tag{5.29}$$

where DIC is usually defined as the sum of an equilibrium mixture of dissolved

$$\mathrm{CO_2, H_2CO_3,\ HCO_3{}^-,\ and\ CO_3^{2-}}.$$

Microbial degradation of DOM and POM could be indicated as (5.30):

$$\begin{aligned}&\mathrm{DOM + POM + microbes \rightarrow H_2O_2 + CO_2 + DIC +\ LOW\ DOM}\\&\mathrm{+ NO_3{}^- + PO_4^{3-} + autochthonous\ DOM +\ other\ species}\end{aligned} \tag{5.30}$$

Products of these reactions are extensively discussed in chapter "Dissolved Organic Matter in Natural Waters", "Photoinduced and Microbial Generation of Hydrogen Peroxide and Organic Peroxides in Natural Waters" and "Photoinduced and Microbial Degradation of Dissolved Organic Matter in Natural Waters", "Colored and Chromophoric Dissolved Organic Matter in Natural Waters", "Fluorescent Dissolved Organic Matter in Natural Waters". The compounds H_2O_2, CO_2, DIC, and nutrients ($NO_3{}^-$ and $PO_4{}^{3-}$) are primarily responsible for an increase in photosynthetic efficiency in water (Eq. 3.1). Therefore photosynthesis depends on the contents and chemical nature of allochthonous OM (of terrestrial vascular plant origin) and autochthonous OM (of algal or phytoplankton origin). They are characterized by a large variation in different water environments (see chapter "Dissolved Organic Matter in Natural Waters"). Dependence of photosynthesis on OM (DOM and POM) is supported by several observation reported below.

First, DOM contents can affect photosynthesis in the water column. DOM can limit productivity and affect epilimnetic and hypolimnetic respiration (Jackson and Hecky 1980; Carpenter et al. 1998; Hanson et al. 2003; Houser et al. 2003; Druon et al. 2010). Both DOM and POM can limit light penetration in deeper water, thus shoaling the euphotic zone (Bertilsson and Tranvik 2000; Laurion et al. 2000; Hayakawa and Sugiyama 2008; Effler et al. 2010). The vertical attenuation coefficient for downward irradiance of PAR (K_{PAR}) is strongly dependent on water color (Eloranta 1978; Jones and Arvola 1984), which subsequently depends on DOC concentration (Jones and Arvola 1984). Elevated DOM may decrease the efficiency of photosynthesis and growth in deeper waters and produce surface Chl *a* maxima in the upper epilimnion (0–8 m). Such an effect has been observed in the lakes Hongfeng, Baihua and Kinneret, and is quite different from Lake Biwa (0–20 m) and Lake Baikal where DOM contents are relatively low (see also chapters "Dissolved Organic Matter in Natural Waters" and "Chlorophylls and Their Degradation in Nature") (Fu et al. 2010; Mostofa KMG et al., unpublished data; Hayakawa 2004; Yacobi 2006). Waters with high contents of DOM and POM are responsible for the occurrence of toxic algal blooms through high photosynthesis. The latter would be linked to elevated amounts of photo- and microbial products, provided that algal growth is limited by nutrient availability and not by light, and would also be affected by global warming (see later).

The second issue is the dependence of photosynthesis on allochthonous DOM. It has been shown that photosynthetic primary production is significantly dependent on allochthonous humic substances (fulvic and humic acids) in natural waters. It has been observed an increase of bacterial biomass with high humic contents (Jones 1992; Tranvik 1988; 1989; Hessen 1985; Tranvik and Höfle 1987). Typhoon-enhanced terrestrial discharges can elevate Chl *a* concentrations by four times and shift phytoplankton composition (spectral class-based), from an initial dominance of diatoms and green microalgae to the dominance of blue green microalgae (cyanobacteria are increased by more than 200 %) and cryptophytes (Blanco et al. 2008). This enhancement is likely caused either by favorable nutrient availability (Blanco et al. 2008) or by high input of allochthonous DOM including humic substances. A higher ratio of bacterial production to primary production has been observed in a humic lake compared with a clear-water lake, suggesting that the bacterioplankton of the humic lake utilized allochthonous substrates in addition to substrates originating from autochthonous primary production (Tranvik 1989). Moreover, a isolated (ca. *Pseudomonas sp.*) bacterial cell does not utilize fulvic acid, but in the presence of added lactate fulvic acid is partially degraded and causes an increase in the cell yield because of co-metabolism (Stabel et al. 1979; Wright 1988; de Haan 1974). Bacteria (ca. *Arthrobacter* sp.) can utilize fulvic acid, but this is only partially degraded and produces a small cell yield compared to e.g. benzoate. However, in media containing benzoate and fulvic acid, bacteria have higher growth rate and cell yield compared to media with only benzoate or fulvic acid (de Haan 1977). The fluctuations in the content of fulvic acids and the amount of benzoate-oxidizing bacteria suggest that the priming effect might be more important than co-metabolism during the decomposition of fulvic acids in lake water (de Haan 1977). The mechanism behind this phenomenon is, presumably, the acceleration of the photoinduced degradation of fulvic acid in the presence of benzoate. It may cause enhanced production of biologically labile substrates that subsequently increase bacterial production. Benzoate (C_6H_5-COONa) may photolytically release electrons (e_{aq}^-) in aqueous solutions of fulvic acid (Fujiwara et al. 1993; Zepp et al. 1987; Assel et al. 1998; Richard and Canonica 2005), an effect that might lead to the production of hydrogen peroxide in natural waters (Mostofa and Sakugawa 2009; Fujiwara et al. 1993).

The generation of hydrogen peroxide (H_2O_2) upon irradiation of ultra-filtered river DOM is substantially increased, from 15 to 368 nM h^{-1}, with increasing salinity at circumneutral pH values (Osburn et al. 2009). Production of $HO^\bullet$ from H_2O_2

either by direct photoinduced reaction ($H_2O_2 + h\upsilon \rightarrow 2HO^\bullet$) or by photo-Fenton processes is susceptible to decompose DOM in aqueous solution (Zepp et al. 1992; Zellner et al. 1990; Goldstein and Rabani 2008). These photoinduced effects are associated with two impacts on growth of primary production: (i) photoinduced generation of $HO^\bullet$ has direct negative effects on bacterial growth and/or indirect effects, because of the loss of bioavailable DOM associated to ROS mineralization (Scully et al. 2003a). Correspondingly, extracellular enzymes (e.g., phosphatase and glucosidase) can be inactivated in natural waters by secondary photoinduced processes that can lead to a reduction of the substrate uptake by bacteria (Scully et al. 2003b; Ortega-Retuerta et al. 2007). (ii) Studies of abundance and growth in the presence of humic substances indicate that bacteria are the most significant utilizers of allochthonous DOM. This issue is apparently made easier by DOM photolysis under natural sunlight, with production of lower molecular weight, and biologically labile organic products (Miller and Zepp 1995; Strome and Miller 1978; Amador et al. 1989; Kieber et al. 1989; Moran and Zepp 1997). This photoinduced effect can be supported by the observation that DOM photobleaching is accompanied by bacterial growth in humic lakes with significant amounts of chromophoric DOM (Lindell et al. 1995; Reche et al. 1998; de Lange et al. 2003). Thus, humic substances in lakes may serve as a substrate for bacterioplankton and lead to enhanced microbial production. Such stimulation of bacterioplankton productivity could influence food chains in two ways (Jones 1992): firstly, by providing an alternative base (in addition to autotrophic primary production) for the energetic and nutritional support of consumer organisms, of course if bacterial production can be effectively grazed; secondly, by increasing bacterial demand for limiting nutrients at the expense of phytoplankton, thereby depressing autotrophic primary production (Jones 1992).

A further issue is the dependence of photosynthesis on autochthonous DOM. Autochthonous DOM or unknown compounds produced by the cyanobacterium *Trichormus doliolum* or filtrates of dinoflagellate *Peridinium aciculiferum* or *Prorocentrum lima* can inhibit the PSII in other cyanobacteria, decreasing the photosynthetic efficiency (Igarashi et al. 1998; Rengefors and Legrand 2001; Sukenik et al. 2002; Windust et al. 1996; von Elert and Juttner 1997; Sugg and VanDolah 1999). Compounds produced by the cyanobacterium *Microcystis* sp. can inhibit carbonic anhydrase activity of the dinoflagellate *P. gatunense*, leading to CO_2 limitation and inhibition of photosynthesis (Sukenik et al. 2002). When tested as a pure compound, okadaic acid produced by the dinoflagellate *Prorocentrum lima* could inhibit the growth of three microalgal species (Windust et al. 1996), possibly because okadaic acid is a potent phosphatase inhibitor (Bialojan and Takai 1988). Also microcystins produced by the cyanobacterium *Microcystis aeruginosa* can inhibit phosphatase (Dawson 1998). Microalgal compounds have been shown to damage red blood cell membranes, which suggest that competing phytoplankton could be similarly affected (Igarashi et al. 1998). On the other hand, autochthonous DOM released by phytoplankton can be utilized with high efficiency by heterotrophic bacteria and can thus stimulate heterotrophic growth and nutrient cycling (Brussaard et al. 1996, 2005, 2007; Gobler et al. 1997; Fuhrman 1992; Bratbak et al. 1998; Middelboe 2003).

Interestingly, the viral lysis of an *Aureococcus anophagefferens* bloom can release approximately 500 g C L^{-1} that can support bacterial demands for both carbon and nutrients (Gobler et al. 1997). It has been shown that >62 % of a bacterial lysate is metabolized by other bacteria following viral lysis within a few days, with a correspondent bacterial growth efficiency of 45 % (Middelboe 2003). Fatty acids potentially produced by microalgae have been shown to increase permeability of the plasma membranes of chlorophytes and cyanobacteria, which might be connected with an increase of photosynthesis (Wu et al. 2006). Photoproduction of biologically labile substrates from CDOM could potentially stimulate the growth of biomass in Hudson Bay coastal waters (Granskog et al. 2007).

Bacterial biomass exhibits high values during the summer season and lower ones during winter in lakes with different water color (Wright 1984; Arvola and Kankaala 1989; Jones 1990). In winter, the bacterioplankton in humic lakes may primarily consist of a dormant, substrate-limited community that may sustain only a small number of microzooplankton grazers (Jones 1992; Wright 1984). During the spring and summer season fresh inputs of labile allochthonous DOM and autochthonous DOM, possibly with enhanced photoinduced activity, stimulate an increase in bacterial production (Jones 1992). In turn, a rapid development is promoted of grazing flagellates until a quasi steady-state is reached, resulting into an active, grazer-controlled bacterioplankton (Wright 1984).

Currently, model results reveal that the progressive release of dissolved organic nitrogen (DON) in the ocean's upper layer during the summer season increases the regenerated primary production by 30–300 % (Druon et al. 2010). This in turn enhances the dissolved organic carbon (DOC) production, mainly deriving from phytoplankton exudation in the upper layer, and the solubilization of particulate organic matter (POM) deeper in the water column (Druon et al. 2010). A microcosm experimental study on summer carbon metabolism in a humic lake has shown that DOC is 80–85 % of total carbon, while 75 % of POC is detritus. Bacterial biomass and production can exceed those of phytoplankton (Hessen et al. 1990). It has been shown that most of the zooplankton body carbon (46–82 %) is apparently derived from direct ingestion of the large detrital carbon pool. The loop of ingestion and defecation is important, giving a detritus particle turnover rate of 0.39 d^{-1}, and suggests that carbon cycling in humic lakes is essentially different from that in clear-water lakes (Hessen et al. 1990).

Finally, both autochthonous and allochthonous DOM contribute to the production of photo- and microbial products (CO_2, DIC, H_2O_2 and so on) and to the photoinduced generation of the reactive oxygen species (ROS) such as $O_2^{\bullet-}$, H_2O_2 and $HO^{\bullet}$ in photosynthesis. Negative effects of photoproducts on bacterial growth are linked with phototransformation of algal-derived autochthonous DOM (Ortega-Retuerta et al. 2007; Tranvik and Bertilsson 2001). This can be supported by the highly photosensitive and photodegradable nature of autochthonous DOM of algal/phytoplankton origin compared to allochthonous DOM (Mostofa et al. 2009; Johannessen et al. 2007). Penetration of sunlight to deep water significantly depends on the DOM contents, and high-DOM lakes are characterized by shoaling of the euphotic zone (Laurion et al. 2000).

Photosynthetic efficiency of phytoplankton decreases as irradiance increases during the morning, and increases as irradiance declines in the afternoon. These trends are associated with photoprotective strategies in the antennae of PSII and photodamage of PSII reaction centers (Zhang et al. 2008). Conversely, H_2O_2 usually shows strong diurnal variation and its concentrations increases gradually from the morning, reaches a maximum at noon and then gradually decreases in the afternoon (Mostofa and Sakugawa 2009). Therefore, high production of H_2O_2 and the subsequent $HO^{\bullet}$ photogeneration (either direct of photo-Fenton mediated) at noon is susceptible to damages PSII reaction centers.

In addition, autochthonous DOM can produce relatively high amounts of ROS that can inhibit primary production. The daily estimated net CO_2 fluxes (due to all processes) are much smaller than daylight photosynthetic rates (^{14}C uptake) and sometimes go in the opposite direction (Kelly et al. 2001). This indicates that CO_2 fixation measured by ^{14}C uptake is largely offset, and sometimes exceeded, by CO_2 production. Allochthonous DOC degradation could account for only a part of this CO_2 production and the remainder presumably comes from the respiration of photosynthetically fixed carbon (Kelly et al. 2001). The average rates of net epilimnetic CO_2 fixation, or net epilimnetic production (NEP) range from 20 to 60 % of ^{14}C uptake (Kelly et al. 2001). This is similar to previous estimates of the relationship between net 24 h and daylight photosynthetic fixation (Berman and Pollingher 1974). Note that NEP is a *community* parameter, including the respiration of grazers, sediment bacteria and so on. Therefore, is not the same as the term "net photosynthesis" that refers only to the photosynthesis and respiration of algae (Kelly et al. 2001).

5.6 Variation in Nutrient Contents

Photosynthesis of organisms is dependent on the contents of nutrients that can either enhance or decrease its efficiency (Parkhill et al. 2001; Liu et al. 2007; Bybordi 2010). The effects of nutrients on photosynthesis can be classified in two ways depending on the types of organisms.

Nutrients Effects on Aquatic Microorganisms

The effect of nutrients on photosynthesis in water may be a stimulation of primary production (Chl *a*), or not (Yoshiyama and Sharp 2006; Parkhill et al. 2001; Smith 2003; Kaneko et al. 2004; Sterner et al. 2004; Huszar et al. 2006; Nõges et al. 2008; McCarthy et al. 2009; Mohlin and Wulff 2009; Canfield 1983; Auclair et al. 1985; Ferris and Tyler 1985; Steinberg and Muenster 1985; Francko 1986; Jones et al. 1988; Lewis 1990; Salas and Martino 1991; Cullen et al. 1992; Sarnelle et al. 1998; Brown et al. 2000; Guildford and Hecky 2000; Jones 2000). Observing the uptake of nutrients during primary production or algal productivity is a complex issue, because of the many factors involved for the demand and supply of N and P in water. Such factors can be classified as follows: (i) Nutrients (NO_3^-, NO_2^-, NH_4^+ and PO_4^{3-}) are mostly released during photoinduced and microbial assimilation or respiration of algal/phytoplankton biomass (Mostofa et al. 2011; Kopáček et al. 2003; Li et al. 2008; Mallet et al. 1998; Carrillo et al. 2002; Lehmann et al. 2004; Fu et al. 2005). (ii) Formation of N-containing (NH_4^+ or NO_2^-) and P-containing inorganic compounds (PO_4^{3-}) typically occurs upon degradation of dissolved organic nitrogen (DON) and dissolved organic phosphorus (DOP) in natural waters (Mostofa et al. 2011; Kim et al. 2006; Li et al. 2008; Bronk 2002; Zhang et al. 2004; Vähätalo and Järvinen 2007; Haaber and Middelboe 2009). The degradation of *Phaeocystis pouchetii* lysates is associated with significant regeneration of inorganic N and P and produces 148 g N L^{-1} and 7 g P L^{-1}, which corresponds to 78 % and 26 % of lysate N and P being mineralized to NH_4^+ and PO_4^{3-}, respectively (Haaber and Middelboe 2009). Contribution of nutrients through viral lysis might be an important mechanism that promotes heterotrophic nutrient cycling and stimulates primary production (Haaber and Middelboe 2009, 2008; Brussaard et al. 2008). (iii) NO_3^- and NO_2^- can be regenerated by oxidation of ammonia in nitrification ($NH_4^+ + 2O_2 \rightarrow NO_3^- + 2H^+ + H_2O$) and of dissolved organic nitrogen (DON) in lake waters (Lehmann et al. 2004; Mack and Bolton 1999; Kopáček et al. 2004; Minero et al. 2007). (iv) NO_2^- and NO_3^- are preferentially detected in epilimnetic water rather than the hypolimnion (Mostofa KMG et al., unpublished data; Kim et al. 2006; Li et al. 2008; Lehmann et al. 2004; Kopáček et al. 2004; Minero et al. 2007), and they are also involved in photoinduced generation of $HO^•$ that is able to degrade DOM in the epilimnion (see also chapters "Photoinduced Generation of Hydroxyl Radical in Natural Waters" and "Photoinduced and Microbial Degradation of Dissolved Organic Matter in Natural Waters") (Mostofa et al. 2009; Nakatani et al. 2007; Takeda et al. 2004; Zellner et al. 1990; Mopper and Zhou 1990). Furthermore, the NO_2^- ion is generally observed at low concentration during the summer season (Mostofa KMG et al., unpublished data; Kim et al. 2006; Li et al. 2008), and possibly it is photolytically more active in production of $HO^•$ than in NO_3^- (see also chapters "Photoinduced Generation of Hydroxyl Radical in Natural Waters" and "Photoinduced and Microbial Degradation of Dissolved Organic Matter in Natural Waters"). It is also a rather photolabile compound in surface waters, undergoing faster direct photolysis in lake than in ultrapure water. This effect is linked to the scavenging of photogenerated transients by DOM, which finally prevents the recombination of photogenerated, transient nitrogen species back into nitrite (Vione et al. 2009a).

Primary production or Chl *a* often increases with increasing total phosphorus (TP) and nutrients, suggesting that uptake of P and nutrients takes place during primary production (Doyle et al. 2005; Huszar et al. 2006; Nõges et al. 2008; McCarthy et al. 2009; Mohlin and Wulff 2009; Guildford and Hecky 2000; Lehmann et al. 2004; Schindler 1974, 2006; Havens et al. 1995; Smith et al. 1995). Chl *a* is significantly correlated with total P in marine environments, but total P concentration in marine sites is relatively higher compared to freshwater (Guildford and Hecky 2000). Uptake of phosphorus during phytoplankton growth is greatly stimulated in presence of humic substances, but the phosphate uptake is inhibited by toxic compounds (Kaneko et al. 2004; Auclair et al. 1985; Steinberg and Muenster 1985; Francko 1986; Jones et al. 1988). Humic substances can easily undergo photoinduced decomposition into several photoproducts such as CO_2, H_2O_2, DIC, LMW DOM, and so on. These compounds are directly and indirectly linked with photosynthesis and can stimulate primary production.

Primary producers or phytoplankton (or Chl *a*) depend on the total nitrogen (TN) as they can uptake both inorganic and organic N forms such as urea, NH_4^+, and NO_3^- (McCarthy et al. 2007, 2009; Walsh and Dugdale 1971; Kappers 1980; Syrett 1981; Dugdale et al. 1990; Probyn 1992; Blomqvist et al. 1994; Berg et al. 2003; Giani et al. 2005; Rolland et al. 2005; Heil et al. 2007). No evidence has been found for a control of Chl *a* by TN in lake and marine environments (Guildford and Hecky 2000). However, TN (mostly NO_3^- and NH_4^+) can limit primary production in most cases where nutrients are limiting (Huszar et al. 2006; Sarnelle et al. 1998; Barica et al. 1980; Smith 1982; Elser et al. 1990; Aldridge et al. 1995; Levine et al. 1997; Philips et al. 1997; Lewis 1996, 2002).

The nutrients-ratio theory predicts that cyanobacteria will dominate in lakes with low TN:TP ratios, due to their superior ability to compete for dissolved N and, in some cases, to fix atmospheric N (Smith 1983). Recent studies show that primary production or cyanobacteria do not follow this predicted theory in a variety of waters, with either high or low TN:TP ratio (Nõges et al. 2008; McCarthy et al. 2009; Xie et al. 2003; Smith et al. 1995; Smith 1983; Smith and Bennett 1999; Downing et al. 2001). The TN:TP ratio theory can not consistently predict cyanobacterial dominance in a variey of waters. Indeed, recent studies show that nutrients such as PO_4^{3-} and NO_3^- are significantly produced from either POM (e.g. phytoplankton) or allochthonous and autochthonous DOM (see chapters "Dissolved Organic Matter in Natural Waters", "Photoinduced and Microbial Degradation of Dissolved Organic Matter in Natural Waters" "Impacts of Global Warming on Biogeochemical Cycles in Natural Waters"). Correspondingly, waters with extreme eutrification are composed of excess PO_4^{3-} that does not follow this theory at all. This can be justified by the observation that primary production is probably not limited by nutrient availability, because of the high nutrient loadings in natural water (McCarthy et al. 2007, 2009; Heath 1992). Primary productivity within a plume appears to rely upon recycled nutrients, with organic fractions representing the majority of the nutrient pool (Davies 2004). Furthermore, remineralized nutrients from the declining chlorophyll bloom in surface waters are taken up by heterotrophic bacteria in the water-column and by benthic microalgae in sediments (Darrow et al. 2003). Variations in DOM and POM contents can greatly modify the contents of nutrients, and additional factors would be involved into the variations of primary production.

Based on these studies, photosynthesis dependence on nutrients is quite complex in natural waters. First, photosynthesis does not depend on nutrients in waters with high contents of DOM and POM, particularly in lakes, estuarine and coastal waters. High content of DOM and POM can often supply the nutrients (NO_3^- and PO_4^{3-}) under both photoinduced and microbial assimilation or degradation, thus the nutrients in excess have no effects on primary production. Second, photosynthesis may depend on nutrients in waters with low contents of DOM and POM.

This effect is the opposite as the previous one, and is most likely accounted for by the low production of nutrients from low contents of DOM and POM.

On the other hand, a decrease in PSII efficiency with changes in cellular physiology of microalgae can result into nutrient (and mostly nitrogen) stress, ultimately followed by a cell stress (Parkhill et al. 2001; Babin et al. 1996; Cullen et al. 1992; Geider et al. 1993; Graziano et al. 1996). These studies thus show that a decrease of photosynthetic efficiency is caused by nutrient stress. Nitrogen stress is found to reduce the maximum quantum yield of carbon fixation (Babin et al. 1996). The mechanism behind the N-containing (NO_2^- and NO_3^-) nutrient stress is presumably that the strong oxidizing agent $HO^\bullet$, photogenerated from both NO_2^- and NO_3^-, could react with the functional groups bound to PSII and can damage the cells. The result is a decline of the overall photosynthetic efficiency that suppresses the primary production. In addition, the synergic effect of UV radiation due to depletion of the stratospheric ozone layer in combination with N-containing nutrient stress can generate extremely high contents of $HO^\bullet$, which can kill aquatic microorganisms. Note that in Antarctic seawater during an ozone hole event, the production of $HO^\bullet$ is enhanced by at least 20 %. Such enhancement would mostly come from nitrate photolysis and to a minor extent from DOM photoinduced reactions (see also chapter "Photoinduced Generation of Hydroxyl Radical in Natural Waters") (Qian et al. 2001).

Nutrients Effects on Higher Plants

Plant growth is enhanced at 200 mg l^{-1} N (as NH_4NO_3) in cvs. (cultivars) 'Licord' and 'Okapi', but it is reduced when the N concentration increases up to 300 mg l^{-1} (Bybordi 2010). Nitrate reductase (NR), a substrate inducible enzyme, is slightly inhibited by salinity in tomato roots, while leaf NR is decreased sharply (Cramer and Lips 1995). In the leaves of tomatoes and cucumbers, NR activity can increase with exogenous nitrate concentration (Martinez and Cerda 1989). NR is decreased in leaves under salinization, which can subsequently decrease NO_3^- uptake by plants under salt stress (Bybordi 2010; Cramer and Lips 1995; Lacuesta et al. 1990; Abd-El Baki et al. 2000). The decreased of nitrate is accompanied by a high Cl^- uptake and low rate of xylem exudation in high osmotic conditions, by either NaCl or other nutrients (Parida et al. 2004; Tabatabaie et al. 2004). Reduced nitrate uptake or translocation can lead to lower NO_3^- concentration in leaves, which can consequently decrease the NR activity under saline conditions.

Several factors (e.g. salinity) can modify the uptake of some nutrients (e.g. Fe, Mn, Cu, Zn, K, etc.), and either increase or decrease their contents in various parts of most plants (Vıllora et al. 2000; Turhan and Eris 2005; Wang and Han 2007; Achakzai et al. 2010; Tunçtürk et al. 2011).

5.7 *Effects of Trace Elements on Aquatic Microorganisms*

Aquatic organisms that carry out photosynthesis are largely affected by trace elements, and PSII is thought to be the primary and most sensitive site of inhibition

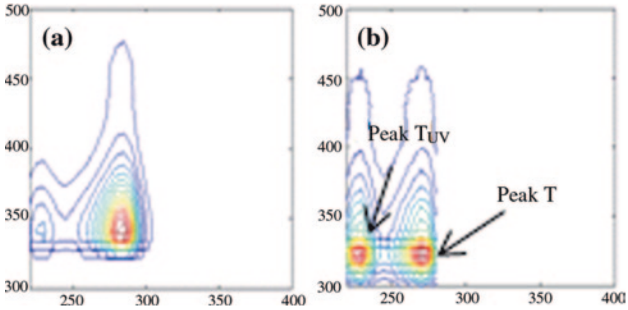


Fig. 10 Two fluorescent components (**a**, **b**) of lake green algae isolated and resuspensions in aqueous media (Milli-Q waters) identified using PARAFAC modeling on the respective EEM data. *Data source* Mostofa KMG et al. (unpublished data)

(Zhang et al. 2010; Crist et al. 1981; Zhou and Wangersky 1985, 1989; Simkiss and Taylor 1989; Xue and Sigg 1990; Tessier and Turner 1995; Sunda and Huntsman 1998; Burda et al. 2003; Koukal et al. 2003; Mylon et al. 2003; Sigfridsson et al. 2004; Berden-Zrimec et al. 2007; Lamelas and Slaveykova* 2007; Hopkinson and Barbeau 2008; Lamelas et al. 2009; Pan et al. 2009). Various trace elements detected in phytoplankton are N, P, S, K, Mg, Ca, Sr, Fe, Mn, Zn, Cu, Co, Cd, Ni, and Mo (Quigg et al. 2003, 2011; Finkel et al. 2006). Study shows that many elements (Fe, Mn, Zn, Cu, Co, and Mo) are enriched relative to P by about two to three orders of magnitude under irradiances that are limiting for growth, and net steady-state uptake of element: P is often elevated under lower irradiances (Finkel et al. 2006). Cyanobacteria or phytoplankton cells can form complexes with or uptake trace metals, either directly or in the presence of humic acids (Zhou and Wangersky 1985, 1989; Xue and Sigg 1990; Koukal et al. 2003; Mylon et al. 2003; Lamelas and Slaveykova* 2007; Lamelas et al. 2009). The latter can substantially enhance the metal ion uptake. Bacteria, algae (or phytoplankton cells) and their exudates are composed of a mosaic of functional groups (e.g. amino, phosphoryl, sulfhydryl, and carboxylic), and the net charge on the cell wall is dependent on the pH of the medium (see also chapter "Complexation of Dissolved Organic Matter With Trace Metal Ions in Natural Waters" for detailed description) (Mostofa et al. 2009; Zhang et al. 2009, 2010; Mostofa et al. 2011; Filella 2008). Cyanobacteria or phytoplankton are composed of two fluorescent components that can be identified using parallel factor (PARAFAC) analysis on the excitation-emission maxima (EEM) spectra of their resuspensions in pure water (Fig. 10) (Mostofa KMG et al. unpublished data). The EEM spectra of these two fluorescent components identify functional groups bound to tryptophan or protein-like components (Fig. 10; see the chapter "Fluorescent Dissolved Organic Matter in Natural Waters" for detailed description) (Mostofa KMG et al. unpublished data). Furthermore, some trace metal ions (e.g., Th^{4+} and U) form complexes at the surface of particulate matter with an organic ligand that might be a nonmetal-specific chelator originating from the cell surface of microorganisms

(Hirose 2004). In addition, autochthonous DOM originating from phytoplankton or algal biomass may contain amino and sulfidic functional groups in its molecular structure, which may form complexes with trace metals in water (Xue and Sigg 1993; Xue et al. 1995).

Fe uptake by phytoplankton is significantly enhanced in the presence of humic substances (Provasoli 1963; Prakash et al. 1973), which is presumably caused by improved metal chelation in aqueous solution (Anderson and Morel 1982). Under low-Fe conditions, Fe allocation in the diatoms *Thalassiosira weissflogii* and *Thalassiosira oceanica* is localized in photosynthetic light–harvesting and electron-transport proteins (Strzepek and Harrison 2004). Increased iron quotas and lowered iron-use efficiencies are often observed in phytoplankton, in response to decreased light levels (Hopkinson and Barbeau 2008; Strzepek and Harrison 2004; Sunda and Huntsman 1997). Iron requirements by phytoplankton increase as available light for photosynthesis decreases, which can lead to the hypothesis that phytoplankton may be colimited by iron and light in low-light environments (Sunda and Huntsman 1997). In an iron–light colimited state growth and photosynthesis are ultimately limited by light processing, whilst production of photosynthetic proteins able to harvest and process light is constrained by iron availability (Hopkinson and Barbeau 2008). Iron– light colimitation may occur in low-iron regions with deep mixed layers, such as the Southern Ocean, or even in macronutrient-limited and stratified waters, near the base of the euphotic zone (Sunda and Huntsman 1997). An iron–light colimitation is observed during winter in the subarctic North Pacific. Here a deep mixed layer (80 m), low incident irradiance, and lack of available iron are all combined to limit photosynthesis, which maintains low phytoplankton biomass (Maldonado et al. 1999). Iron can limit growth in an area with a relatively shallow (40 m) mixed layer in the Subantarctic Front. However light, in conjunction with iron, can control growth in an area with deeper (90 m) mixed layers (Boyd et al. 2001). Iron–light colimitation should also be a factor influencing phytoplankton growth during the North Atlantic spring bloom (Moore et al. 2006).

Availability of iron alone has also been implicated as an important factor in the bloom of some harmful algal species (Bruland et al. 2001; Maldonado et al. 2002), whilst an increase in the toxicity of *Microcystis aeruginosa* has been observed when iron is limited (Lukač and Aegerter 1993). Iron deficiency can affect the electron transfer rate in *Pisum sativum* chloroplasts (Muthuchelian et al. 2001), and stable organic Fe(III) complexes (FeL) photolytically produce dissolved inorganic iron at a higher extent than thermal decomposition and cell-surface reduction of FeL. Such a process can facilitate phytoplankton uptake of iron in the ocean (Fan 2008). On the other hand, during nighttime the reactive oxygen species (H_2O_2 and $O_2^{\bullet -}$) produced by reductases on cell surfaces react with FeL, producing Fe(II). Such a process slows down the oxidation of Fe(II) and the subsequent formation of FeL, thereby maintaining significant levels of bio-available Fe (Fan 2008).

A significant effect of toxic metals on photosynthesis is observed, and the relevant photosynthetic efficiency can be either enhanced or suppressed in natural waters (Zhang et al. 2010; Burda et al. 2003; Koukal et al. 2003; Sigfridsson et al. 2004; Berden-Zrimec et al. 2007; Pan et al. 2009; Mayer et al. 1997; Horton and

Bowyer 1990; Prasad et al. 1991; Barraza and Carballeira 1999; Susplugas et al. 2000; Appenroth et al. 2001; Franklin et al. 2001; Drinovec et al. 2004; Miller-Morey and van Dolah 2004; Shanker et al. 2005; Alam et al. 2007; Hayat et al. 2007; Perales-Vela et al. 2007; Ali et al. 2008; Hasan et al. 2008; Vernay et al. 2008). The esterase activity in several species of marine and freshwater cyanobacteria can be either enhanced or suppressed by copper (Franklin et al. 2001), and antimony (Sb) exposure at concentrations ranging from 1.0 to 10.0 mg L^{-1} inhibits O_2 evolution (Zhang et al. 2010). A decrease in photosynthetic efficiency is caused by the reduction of phytoplankton enzyme activity, which may be a general indicator of cell stress. The stimulating action of Cu for a definite concentration level (e.g. 0.02 mg Cu L^{-1}) on PSII system is often observed in natural waters (Franklin et al. 2001; Burda et al. 2002; Schaffer and Sebetich 2004).

Toxicity of Cd and Zn to the green alga *Pseudokirchneriella subcapitatais* can be significantly ($p < 0.05$) reduced in the presence of humic acids (soil and peat), but not in the presence of Suwannee River fulvic acid (SRFA) (Koukal et al. 2003). It is postulated that humic acid can reduce Cd and Zn toxicity in two different ways (Koukal et al. 2003): (i) Humic acid is capable of decreasing the amount of free metal ions through complex formation with the metal. Humic acid has high molecular weight and is relatively stable with regard to metal-exchange reactions, which can make the metals less bioavailable. (ii) Humic acid can be adsorbed onto algal surfaces, shielded the cells from free Cd and Zn ions. On the other hand, several hypotheses have been advanced to explain why SRFA is unable to reduce metal toxicity (Koukal et al. 2003): (i) Cd- and Zn-SRFA complexes are thought to be labile (i.e. to undergo rapid dissociation); (ii) SRFA can coagulate, presumably during equilibration, which can alter their metal complexing behavior; and (iii) SRFA has a low ability to adsorb on cell membranes at pH > 7.

For better understanding the mechanism of metal toxicity to organisms, it is interesting to have a look at the outer-shell electronic configurations of toxic metals:

As^{33}: $1s^22s^22p^63s^23p^63d^{10}4s^24p^3$ and As^{3+}: $1s^22s^22p^63s^23p^63d^{10}4s^24p^0$;

Sb^{51}: $1s^22s^22p^63s^23p^63d^{10}4s^24p^64d^{10}5s^25p^3$ and Sb^{3+}:$1s^22s^22p^63s^23p^63d^{10}4s^2 4p^64d^{10}5s^25p^0$;

Zn^{30}: $1s^22s^22p^63s^23p^63d^{10}4s^2$ and Zn^{2+}: $1s^22s^22p^63s^23p^63d^{10}4\,s^0$;

Cd^{48}: $1s^22s^22p^63s^23p^63d^{10}4s^24p^64d^{10}5\,s^2$ and
Cd^{2+}: $1s^22s^22p^63s^23p^63d^{10}4s^24p^64d^{10}5\,s^0$;

Cr^{24}: $1\,s^2\,2s^22p^6\,3s^23p^64\,s^1\,3d^5$ and Cr^{4+}: $1\,s^2\,2s^22p^6\,3s^23p^64s^13d^1$

Cu^{29}: $1\,s^2\,2s^22p^6\,3s^23p^64\,s^1\,3d^{10}$ and Cu^{2+}: $1\,s^2\,2s^22p^6\,3s^23p^64s^13d^8$

These metal ions have empty *s*-, *p*- or *d*-orbitals in the outer shell, which allows them to be involved in a strong π–electron bonding system through donation of electrons from the functional groups of PSII (e.g. N- and S-containing carboxylic, amino, thio and hydroxyl groups) (see chapter "Complexation of Dissolved Organic Matter With Trace Metal Ions in Natural Waters" for detailed discussion)

(Mostofa et al. 2009, 2011). After formation of the strong π–electron bonding system in the metal-protein (or organism) complex, the remaining outer-shell electrons (e.g. $4s^2$ for As) are loosely bound and can easily move (see chapter "Complexation of Dissolved Organic Matter With Trace Metal Ions in Natural Waters" for detailed explanation). After complex formation between metals and proteins (or amino acids) in PSII, the normal cells metabolism can be disrupted by electrons in the outer shell of the metal ion itself, or via $HO^{\bullet}$ formation in Fenton or Fenton-like or other unknown processes, finally leading to cell death.

Interestingly, As-protein complexes may be accumulated in the human skin and, when the skin is exposed to natural sunlight (mostly UV-light), irradiation induces the formation of $HO^{\bullet}$ or other reactive oxygen species (e.g. $O_2^{\bullet -}$ and H_2O_2). These species can cause damage to DNA and finally induce cancer in the human body. Coherently, it has been suggested that DNA damage induced by methylated trivalent arsenicals is mediated by reactive oxygen species (Nesnow et al. 2002). Furthermore, arsenite can play a role in the enhancement of UV-induced skin cancers (Rossman et al. 2004). The carcinogenic effects may be connected with accumulation of As^{3+} or Sb^{3+} and other toxic metals. As^{3+} or Sb^{3+} have two electrons in the outer shell, while their inner shells are entirely filled with electrons. This situation makes the outer-shell electrons of metal-protein complexes highly mobile.

As and cigarette smoke are synergistic, producing an elevated risk of bladder and lung cancer in smokers (Hopenhayn-Rich et al. 1998; Steinmaus et al. 2003; Chen et al. 2004). Smoking could help promoting the excitation of electrons from the outer shells of As in As-protein complexes, which can finally induce formation of $HO^{\bullet}$ that damages DNA. While eating soil is quite unusual for humans, in some rural Bangladesh villages it is customary for pregnant women to eat *shikal* (it sounds like "chain" in English), which consists of small (2 in. × 1 in. × 1/2 in.) pellets made out of flooded soil (information source is personal experience of one of the authors). While the origin of this tradition is quite uncertain, it is noteworthy that it was observed in one of the world's regions where human exposure to As is the highest. Interestingly, intake of black soil (dark brown soil) with high contents of humic acid could reduce As levels in the human body, because complexes between As and humic acids are much stronger than As-protein or As-fulvic acids ones (see chapter "Complexation of Dissolved Organic Matter With Trace Metal Ions in Natural Waters" for detailed discussion).

Coming back to photosynthetic microorganisms, the decrease in photosynthetic efficiency can be cause by complex formation between metals and the functional groups of PSII. Two possible mechanisms can be operational. First, the formed metal-cells or metal-proteins complexes in the PSII of aquatic microorganisms can produce electrons (e^-) photolytically upon exposure to sunlight, which can finally lead to H_2O_2 generation. (see chapter "Photoinduced and Microbial Generation of Hydrogen Peroxide and Organic Peroxides in Natural Waters" for detailed mechanism) (Komissarov 2003; Mostofa and Sakugawa 2009; Mostofa et al. 2011; Fujiwara et al. 1993). Coherently, it has been observed that methyl viologen acts as an inducer of photo-oxidative stress (Donahue et al. 1997; Mano et al. 2001) and can induce the photoreduction of dioxygen (O_2) by accepting electrons from the iron-sulfur cluster Fe-S_A/Fe-S_B of PS1. This process could induce the production of superoxide radical ($O_2^{\bullet -}$) and H_2O_2 (Fujii et al. 1990). When catalytic free metals [e.g., Fe(II), Cu(I) and Mn(II)] are present near the production site of $O_2^{\bullet -}$ and H_2O_2, the strong oxidizing agent $OH^{\bullet}$ can be produced via a Fenton reaction or by direct photodissociation (Zepp et al. 1992; Nakatani et al. 2007; Zellner et al. 1990; Goldstein and Rabani 2008; Halliwell and Gutteridge 1984; Stadtman 1993). The photo-Fenton reaction could proceed as follows (Eqs. 5.31, 5.32):

$$Fe^{3+} + h\upsilon/H_2O^{\bullet}/O_2^{\bullet -} \rightarrow Fe^{2+} + O_2 + H^{+} \tag{5.31}$$

$$Fe^{2+} + H_2O_2 + h\upsilon \rightarrow Fe^{3+} + HO^{\bullet} + OH^{-} \tag{5.32}$$

The $HO^{\bullet}$ radical thus generated kills the cells of microorganisms in natural waters. Fe concentration and pH can significantly affect both the growth and the reactive oxygen species (ROS) production in *Chattonella marina*, a harmful algal bloom species (Liu et al. 2007). The rapid photoinduced release of electrons from the outer shell of metal ions in PSII metal-protein complexes can be involved in chronic toxicity. It has recently been shown that exposure of PSII to Sb^{3+} and Cr^{4+} in *Synechocystis* sp. can increase the dissipated energy flux and decrease the performance index and the maximum quantum yield for primary photochemistry (φP_O) (Zhang et al. 2010; Pan et al. 2009). It can also cause damage to cellular components and to the overall photosynthetic driving force. The fluorescence yield at 684 nm, which is connected to the maximum quantum yield for primary photochemistry (Zhang et al. 2010) is affected by the metal-functional groups of PSII. It can be the easiest way by which electrons are released, which can subsequently result into high production of $HO^{\bullet}$ via $O_2^{\bullet -}$ or H_2O_2. Such a process can decressee photosynthetic efficiency or damage the PSII or DNA. Along with this effect, complexation between metal ions and the functional groups of PSII can inhibit electron transport and cause the overall photosynthetic efficiency to decline. Severe damage in the water-splitting site of PSII can produce an increased ratio of F_O / F_V (fluorescence level before and after flash) (Pan et al. 2009), which may occur because of $HO^{\bullet}$ photoproduction. Note that Sb^{3+} compounds are approximately ten times more toxic than Sb^{5+} ones, possibly because of the two unpaired electrons in Sb^{3+} species. In contrast, Sb^{5+} species have no outer shell electrons.

Another possible effect linked with complex formation between metals and the functional groups bound to PSII is the blockage of the normal function of electron release by PSII-bound functional groups. This can also significantly decrease the photosynthetic efficiency of aquatic organisms.

The stimulating effect of Cu^{2+} ($1s^2\ 2s^2 2p^6\ 3s^2 3p^6 4s^1 3d^8$) on PSII is presumably caused by the partially and completely filled outer shell of its *s*- and *d*-orbitals. Therefore, the complexes formed between Cu^{2+} and the PSII functional groups are not as strong as those involving other metal ions with empty orbitals. This effect can roughly recover the normal function of PSII in organisms. In addition, the electrons released from the metal-protein complexes of PSII can induce the generation of relatively low amounts of H_2O_2, which might enhance photosynthesis in aquatic organisms. Further studies will be needed to evaluate the exact mechanism behind this phenomenon. The formation of complexes between metals and the functional groups of either PSII or PSI is a relatively new hypothesis, which could greatly help improving the present understanding of the effects of metal ions on the photosynthetic efficiency of aquatic organisms.

5.8 Effect of Salinity or Salt Stress

Salinity is an important controlling factor for photosynthesis, its effect depending on the organisms such as higher plants or aquatic microorganisms. Therefore, the effect of salinity can be divided into two classes: (i) effect on aquatic microorganisms; (ii) effect on higher plants.

Effects of Salinity on Aquatic Microorganisms

Water salinity or salt stress has a significant impact on the photosynthetic capability of organisms, but the actual effect is highly dependent on the different kinds of microorganisms (Liu et al. 2007; Satoh et al. 1983; Ahel et al. 1996; Moisander et al. 2002; Marcarelli et al. 2006; Segal et al. 2006; Demetriou et al. 2007; Allakhverdiev and Murata 2008). It has been shown that salinity in marine waters can alter the PSI and PSII of organisms, which is connected to salt stress. However, some organisms such as cyanobacteria or phytoplankton can overcome the salt stress and are capable of growing under salinity conditions which would be harmful to most other organisms. The basic physiological responses of cyanobacterial cells to salt stress occur in three phases (Hagemann and Erdmann 1997). First, within seconds an increase of the ambient concentration of NaCl can cause an influx of Na^+ and Cl^- ions into the cytoplasm. Second, within an hour it starts the replacement of Na^+ by K^+ ions, leading to a decline in the toxic effects of high Na^+ concentrations. Third, within several hours the cells become acclimatized to the elevated ion concentrations. During this phase, the synthesis or uptake of compatible solutes/components mitigates the toxic effects of salts and preserves the structures of complex proteins and cell membranes (Bhagwat and Apte 1989; Reed et al. 1985; Hagemann et al. 1990, 1991; Hayashi and Murata 1998; Chen and Murata 2002). The cyclic electron transport via PSI is also activated (Joset et al. 1996; Hibino et al. 1996). However, over a longer period of time, such as within several days, salt stress can inhibit cell division (Ferjani et al. 2003).

The increase in the intracellular concentrations of Na^+ and Cl^- ions can cause irreversible inactivation of the oxygen-evolving machinery and of the electron-transport activity of PSI (Kuwabara and Murata 1983; Miyao and Murata 1983; Murata and Miyao 1985; Allakhverdiev et al. 2000a, b). For instance, incubation of *Synechococcus* cells with 0.5 M NaCl can suppress the reduction of P700$^+$ (Allakhverdiev et al. 2000a). Because P700$^+$ is reduced by plastocyanin, it is suggested that the association of this compound with the PSI complex is disturbed by the presence of NaCl (Allakhverdiev et al. 2000a, b).

In cyanobacteria, the oxygen-evolving machinery of PSII located on the luminal side of thylakoid membranes is stabilized by three extrinsic proteins. They are PsbO (33-kD protein), PsbV (cytochrome c_{550}), and PsbU (Allakhverdiev and Murata 2008; Shen et al. 1998; Nishiyama et al. 1999). Cyt c_{550} and PsbU are loosely bound to the donor side of the core complex of PSII (Nishiyama et al. 1997, 1999). These proteins could be easily dissociated from the cyanobacterial PSII complex in the presence of elevated concentrations of NaCl (Shen et al. 1998, 1992). Moreover, pulse-chase experiments revealed that salt stress can inhibit the de novo synthesis of D1 in *Synechococcus* (Ohnishi and Murata 2006).

Light is an important factor in restoring the activity of PSII and PSI during dark incubation of cyanobacterial cells under salt stress (Allakhverdiev et al. 2005). When light is applied to *Synechococcus* cells, protein synthesis occurs for the recovery of the photosystems from salt stress (Allakhverdiev and Murata 2008; Hagemann et al. 1991; Allakhverdiev et al. 1999, 2005). Weak light at 70 mE m^{-2} s^{-1} is sufficient to generate ATP, which seems to support recovery (Allakhverdiev and Murata 2008). Such conditions are sufficient to induce the necessary excitation, because of the formation of complexes between cations (e.g. Na$^+$ and other cations from salts) and the functional groups bound to PSII and PSI. Recent studies of PSII photoinhibition in cyanobacteria suggest that oxidative stress due to reactive oxygen species (ROS) can inhibit protein synthesis and the repair of PSII. However, it does not stimulate photodamage to PSII (Nishiyama et al. 2005, 2006; Takahashi and Murata 2008; Murata et al. 2007). Note that salinity in marine waters is accounted for various salts including NaCl (86 %), but comparison of river and sea water shows that Na$^+$, Ca^{2+}, Mg^{2+}, K$^+$, HCO$_3^-$, Cl$^-$ and SO$_4^{2-}$ in the sea are typically 1,670, 27, 330, 170, 2.4, 2,400 and 245 times, respectively, higher than in rivers (see chapter "Complexation of Dissolved Organic Matter With Trace Metal Ions in Natural Waters" for more discussion). Also note that the occurrence of these salts can cause changes in the absorption properties of chromophoric dissolved organic matter (CDOM), and in the fluorescence properties of fluorescent dissolved organic matter (FDOM). A change in the optical properties (generally shifting from shorter towards longer wavelengths) and in the complexation behavior of both CDOM and FDOM can be linked to an enhanced photoinduced generation of H_2O_2 (see chapters "Photoinduced and Microbial Generation of Hydrogen Peroxide and Organic Peroxides in Natural Waters" "Colored and Chromophoric Dissolved Organic Matter in Natural Waters", "Fluorescent Dissolved Organic Matter in Natural Waters", and "Complexation of Dissolved Organic Matter With Trace Metal Ions in Natural Waters", respectively for their detailed discussion).

A proposed mechanism for the decline of photosynthesis of microorganisms is that cations (e.g. Na$^+$, Ca^{2+}, Mg^{2+}, Sr^{2+}) of various salts occurring in marine waters can form complexes with functional groups bound to microorganisms (or with their PSII). This complexation can decrease photosynthesis, either by inducing high photoinduced formation of $HO^{\bullet}$ from H_2O_2, which would damage PSII, or by blocking the normal function of electron release by the PSII functional groups. Either effect could alter the normal function of PSII, as extensively discussed in an earlier section (see the "effect of trace metal ions" section). In addition, complexes of trace metal ions in marine waters with autochthonous DOM of algal/phytoplankton origin and with terrestrial DOM of vascular plant origin can induce rapid photoinduced excitation of electrons (e^-). Such a process can produce $O_2^{\bullet-}$, H_2O_2 and $HO^{\bullet}$ that can subsequently either decompose the proteins and the functional groups bound to microorganisms, decreasing their photosynthetic efficiency, or transform the DOM components with production of a number of photoproducts such as CO_2, DIC, H_2O_2 and LMW DOM. These products are directly linked with an enhancement of photosynthesis and might account for algal blooms, particularly in coastal marine environments.

This mechanism is supported by earlier studies, showing that the inhibition of electron flow on the oxidizing (water) side of PSII causes photoinhibition. Moreover, photoactivation and dark-inactivation of electron flow on the reducing side of PSI is completely inhibited at high salinity (Satoh et al. 1983). It is known that photobleaching of carotenoids and Chl can take place when the oxidizing side of PSII is inhibited (Yamashita et al. 1969; Katoh 1972). It has also been observed that inhibition on the reducing side of PSI can give rise to strong reductants, which can also destroy the reaction centers of both PSI and PSII (Satoh and Fork 1982a, b). Photobleaching of carotenoids and Chl might be caused by $HO^{\bullet}$ or other oxidants, generated photolytically by the above mechanism, in analogy with the well-known phenomena concerning DOM photobleaching in natural waters (see chapters "Photoinduced Generation of Hydroxyl Radical in Natural Waters", "Photoinduced and Microbial Degradation of Dissolved Organic Matter in Natural Waters", "Colored and Chromophoric Dissolved Organic Matter in Natural Waters", and "Fluorescent Dissolved Organic Matter in Natural Waters" for detailed discussion).

Effects of Salinity on Higher Plants

Salinity of soil or water is one of the key environmental factors that limit plant growth and productivity, particularly in arid, semi-arid and freshwater land near coastal regions. Salinity can have a two-fold effect on plants: (i) osmotic stress, by which salt in the soil can reduce the availability of water to the roots, and (ii) ionic stress due to the salt taken up by the plant that can be accumulated to toxic levels in certain tissues (Munns et al. 1995). Reduction of photosynthesis caused by salt stress has an impact on several physiological responses, such as inhibition of growth and development, modification of ion balance, mineral nutrition, water status, stomatal behavior, decrease in photosynthetic efficiency and in chlorophyll content (which leads to a corresponding reduction of light absorption by leaves), decrease of carotenoids, carbon allocation and utilization, net carbon dioxide exchange, respiration and protein synthesis, and finally, induction of cell expansion in both roots and leaves in salt-sensitive plants (Bybordi 2010; Tunçtürk et al. 2011; Melgar et al. 2008; Pandey and Yeo 2008; Pandey et al. 2009; Bybordi et al. 2010a, b; Flowers et al. 1977; Munns and Termaat 1986; Zidan et al. 1990; Ashraf and Wu 1994; Neumann et al. 1994; Evans 1996; Jungklang et al. 2003; Meloni et al. 2003; Qiu and Lu 2003; Lee et al. 2004; Pal et al. 2004; Suwa et al. 2006; Ali et al. 2007; Desingh and Kanagaraj 2007; Šiler et al. 2007; Ahmed et al. 2008). It has been shown that some physiological responses (e.g. chlorophyll and carotenoids) are initially increased at moderate NaCl levels, but they are generally decreased by increasing salinity. It has also been observed that cations or metal ions in all plant parts are typically increased with an increase in salt stress.

The effects of salinity are mostly linked to a decrease in stomatal conductance and/or to the non-stomatal limitation related to carbon fixation (Bongi and Loreto 1989; Brugnoli and Björkman 1992; Delfine et al. 1998, 1999; Centritto et al. 2003). It is suggested that stomatal limitation prevails at intermediate salinity levels, while the non-stomatal limitations predominate under severe salt stress conditions (Bongi and Loreto 1989). The photosynthetic rate, PSII efficiency, root and shoot growth of *Centaurium erythraea* is increased or remains the same at moderate salt levels (50–200 mM NaCl), but it is decreased significantly at high salt concentration (400 mM NaCl). Root growth is more adversely affected by increasing NaCl concentration than shoot growth (Šiler et al. 2007). Chlorophyll contents are decreased under elevated salinity conditions for some salt-sensitive plant species, but they are not modified at moderate salt levels (Jungklang et al. 2003; Lee et al. 2004; Šiler et al. 2007; Delfine et al. 1998, 1999; Ashraf et al. 2002). This suggests that the decline of chlorophyll content depends on the salinity level, on the time of exposure to salts and on the plant species. Salinity can rapidly inhibit root growth and subsequently decrease the uptake of water and essential mineral nutrients from soil (Neumann 1997). An increase of NaCl concentration in solution can reduce N and NO_3 concentrations in leaves, when plants are treated with NaCl and NH_4NO_3 (Bybordi 2010). An apparent increase in salt tolerance is observed when N levels, supplied under saline conditions, exceed the optimum ones observed under non-saline conditions (Bybordi et al. 2010a; Papadopoulos and Rendig 1983). This indicates that increased fertilization, especially by N, may improve the deleterious effect of salinity (Ravikovitch and Porath 1967).

A contribution to salt stress in salt-sensitive plants may derive from the fact that an increase of salinity can enhance the metal ion contents in plant cells, because metal ions can form complexes with PSII functional groups. As already mentioned, such a complexation may cause either a high production of photoinduced electrons (e^-) and of superoxide anion ($O_2^{\bullet -}$), H_2O_2 and $HO^\bullet$, which can damage PSII, or block further photoinduced generation of electrons from PSII itself.

Conversely, the plant growth at moderate levels of NaCl might also be favored by photoinduced generation of H_2O_2 from PSII-metal complexes. If moderate, such H_2O_2 levels could be favourable to photosynthesis as discussed before (Eq. 3.1). The balance is delicate, however, because excessive salt can cause high production of H_2O_2 and $HO^\bullet$ that can damage the PSII. These proposed mechanisms can be justified by the observation of several physiological functions caused by salt stress, such as: (i) salinity stress in plants can produce reactive oxygen species (ROS) such as $O_2^{\bullet -}$, H_2O_2 and $HO^{\bullet}$, particularly in chloroplasts and mitochondria (Mittler 2002; Masood et al. 2006). Plants possess a number of antioxidant enzymes such as superoxide dismutase (SOD), ascorbate peroxidase (APX) and glutathione reductase (GR) for protection against the damaging effects of ROS (Asada 1992; Prochazkova and Wilhelmova 2007), but ROS-linked salinity stress can cause membrane disorganization, metabolic toxicity and attenuated nutrients (Frommer et al. 1999; Zhu 2000; Costa et al. 2005) These initial effects can then induce more catastrophic events in plants. Excessive salt stress can eventually cause photoinhibition and photodamage of PSII (Krause and Weis 1991; Belkhodja et al. 1994). (ii) Strong salt stress in salt-sensitive species can severely reduce the potential of electron transport in PSII (Jungklang et al. 2003). (iii) Salinity can increase or decrease uptake of some nutrients (e.g. Fe, Mn, Cu, Zn, K, etc.) depending on the plant species (Vıllora et al. 2000; Turhan and Eris 2005; Wang and Han 2007; Achakzai et al. 2010; Tunçtürk et al. 2011; Greenway and Munns 1980; Martinez et al. 1987; Cornillon and Palloix 1997; Alpaslan et al. 1998). The increase in these metals can enhance complexation with the PSI and PSII functional groups, leading to ROS production. High Na^+ content is generally responsible for alteration of the nutrient balance, which can cause specific ion toxicity in addition to disturbing the osmotic regulation (Greenway and Munns 1980). (iv) Due to the complex formation between metals and PSII functional groups, electron excitation at low irradiance can induce effective generation of H_2O_2 and ROS. This can be justified by the in vivo observation of ROS generation inside PSII membranes. Salt stress may thus damage the photosynthetic activity of PSII even at low irradiance (Pandey et al. 2009). (v) Complexation of trace metal ions with functional groups bound to PSII under salinity conditions can enhance electron release and, as a consequence, ROS production (see chapter "Complexation of Dissolved Organic Matter With Trace Metal Ions in Natural Waters"). Such effects are able to photodamage PSII in *Chlamydomonas reinhardtii*, barley leaves (*Hordeum vulgare*), sorghum (*Sorghum bicolor*), rye (*Secale cereal*), and *Spirulina platensis* (Neale and Melis 1989; Sharma and Hall 1991; Hertwig et al. 1992; Lu and Zhang 1999).

Chl content in salt-tolerant plants would either remain the same or be significantly enhanced with increasing salinity (Qiu and Lu 2003; Brugnoli and Björkman 1992), and accumulation of compatible solutes (e.g. proline, betaine, polyols, sugar alcohols, and soluble sugars) in many plants can increase the tolerance of PSI and PSII to salt stress (Chen and Murata 2002; Fulda et al. 1999; Zhu 2002; Reed and Stewart 1988). The increase of Na^+ and Cl^- ions in both leaves and roots is accompanied with an increase in proline and soluble sugars which could play a role in salt tolerance (Melgar et al. 2008; Ahmed et al. 2008).

While functioning in an otherwise similar way as non-tolerant plants, salt-tolerant plant species may supply relatively low amounts of salt ions to leaves through roots. The consequence may be the occurrence of relatively low contents of H_2O_2. If the latter be present in moderate amount, it would mostly be used in photosynthesis and would not produce dangerous levels of $HO^{\bullet}$. Therefore, the plant may maintain normal photosynthesis in the presence of high salt levels. Salt tolerance in canola is associated with the ability to reduce uptake and/or transport of saline ions (Bybordi 2010).

In addition, resistance to salinity may occur when a plant is capable of producing large amounts of antioxidant enzymes such as superoxide dismutase (SOD), ascorbate peroxidase (APX) and glutathione reductase (GR) (Asada 1992; Prochazkova and Wilhelmova 2007; Mittova et al. 2002; Gossett et al. 1994; Pastori and Trippi 1993). These enzymes can significantly scavenge free radicals under stress conditions.

Elevated levels of GR are capable of increasing the amount of $NADP^+$, which accepts electrons from the photosynthetic electron transport chain (Peltzer et al. 2002; Reddy et al. 2004). The activity of antioxidant enzymes under saline conditions are typically increased in the case of salt-tolerant cotton varieties, shoot cultures of rice, cucumber, wheat shoot and pea (Bybordi et al. 2010b, c; Meloni et al. 2003; Desingh and Kanagaraj 2007; Fadzilla et al. 1997; Lechno et al. 1997; Hernandez et al. 1999; Meneguzzo et al. 1999). Due to salinity stress, plants can accumulate osmolytes such as proline and glycine betaine, which are known to protect macromolecules by stabilizing protein structure during dehydration and/or by scavenging ROS produced under stress conditions (Desingh and Kanagaraj 2007; McNeil et al. 2001; Zhu 2001; Matysik et al. 2002; Rontein et al. 2002). Tolerance of photosystems to salt stress can be enhanced by genetically engineered increase in the unsaturation of fatty acids in membrane lipids, and by intracellular synthesis of compatible solutes (e.g. glucosylglycerol and glycinebetaine) (Allakhverdiev and Murata 2008). When photosynthetic organisms are exposed to salt stress, fatty acids of membrane lipids are desaturated (Huflejt et al. 1990). Therefore, unsaturation of fatty acid in membrane lipids can enhance tolerance of PSI and PSII to salt stress (Allakhverdiev and Murata 2008).

Enhanced tolerance of PSII to salt stress upon unsaturation of membrane lipids is probably accounted for by the fact that unsaturated fatty acids are generally capable of surrounding the cations [e.g. Na^+/H^+ antiporter(s) and/or H^+-ATPase(s)] with their electron-rich double bonds. An increase in the levels of the antiport system components can decrease the concentration of Na^+ ions in the cytosol, which may protect PSII and PSI against NaCl-induced inactivation (Allakhverdiev and Murata 2008).

5.9 *Effects of Toxic Pollutants on Aquatic Microorganisms*

Environmentally-occurring toxic organic pollutants can decrease the efficiency of photosynthesis, most presumably by adversely affecting the PSII (Berden-Zrimec et al. 2007; Mayer et al. 1997; Halling-Sørensen et al. 2000; Katsumata et al. 2005, 2006; Kvíderová and Henley 2005; Zrimec et al. 2005; Pan et al. 2009; Yates and Rogers 2011). Some antibiotics (e.g. ampicillin, streptomycin, levofloxacin hydrochloride, mecillinam, trimethoprim, ciprofloxacin), phenols (e.g. 3,5-dichlorophenol), pesticides and herbicides (e.g. DCMU or diuron, simazine, atrazine) are highly toxic to microorganisms such as cyanobacteria or phytoplankton cells (Berden-Zrimec et al. 2007; Halling-Sørensen et al. 2000; Katsumata et al. 2005, 2006 Kvíderová and Henley 2005; Zrimec et al. 2005; Pan et al. 2009; Yates and Rogers 2011; DeLorenzo et al. 2001). The toxic organic compounds are effective in inhibiting O_2 evolution and PSII activity of microorganisms. The inhibitory effect on PSII is often increased with increasing concentration of toxic compounds. Levofloxacin hydrochloride, one of the most commonly used fluoroquinolone antibiotics, can decrease the density of the active photosynthetic reaction centers of *Synechocystis* sp., inhibit electron transport, and increase the dissipated energy flux per reaction center. All these effects together are able to decrease the photosynthetic efficiency (Pan et al. 2009).

The adverse effect on photosynthesis is thought to be caused by two facts. First, the molecular structures of organic contaminants are mostly composed of N-, S-, O-, and/or P-containing functional groups, which are susceptible to form H-bonding with the functional groups of PSII. This effect can decrease the efficiency of electron release from PSII. It has in fact been demonstrated that the herbicide DCMU can directly block the electron transport in PSII (Berden-Zrimec et al. 2007; Tissut et al. 1987; Behrenfeld et al. 1998). The second issue is that N-, S-, O-, or P-containing functional groups can release electrons upon excitation by light, which can produce ROS such as $O_2^{\bullet -}$, H_2O_2 and $HO^{\bullet}$. These oxidizing species can damage the PSII system, thereby reducing the photosynthetic efficiency as a whole.

KCN (an inhibitor of mitochondrial respiration) and 3-(3,4-dichlorophenyl)-1,1-dimethylurea (an inhibitor of photosynthesis) had no significant effects on ROS production. In contrast, vitamin K3 (a plasma membrane electron shuttle) can enhance ROS production and its antagonist, dicumarol, can decrease it (Liu et al. 2007). Photosynthetic organisms can produce ROS by activating various oxidases and peroxidases, in response to environmental stresses such as pathogens, drought, light intensity, an increase in temperature from 7 °C to 30 °C, and contaminants such as paraquat (Peng and Kuc 1992; Moran et al. 1994; Karpinski et al. 1997; Iturbe-Ormaetxe et al. 1998; Twiner and Trick 2000).

5.10 Effect of Size-Fractionated Phytoplankton

Planktonic algae of $<5\,\mu m$ in size are major fixers of inorganic carbon in the ocean and dominate phytoplankton biomass in post-bloom, stratified oceanic temperate waters (Li 1994; Tarran et al. 2001). Large and small algae are viewed as having a critical growth dependence on inorganic nutrients. The latter can be assimilated at lower ambient concentrations due to the higher surface-area-to-volume ratios of small vs. larger organisms (Malone 1980; Chisholm 1992; Zubkov and Tarran 2008). Experimental studies that adopted phosphate tracer suggest that small algae can uptake inorganic phosphate indirectly, possibly through feeding on bacterioplankton (Hansen and Hjorth 2002; Stibor and Sommer 2003; Tittel et al. 2003; Unrein et al. 2007; Zubkov et al. 2007; Jones 2000; Bird and Kalff 1986; Arenovski et al. 1995; Rothhaupt 1996; Thingstad et al. 1996; Caron 2000). Inorganic phosphate and other nutrients (e.g. NO_3^-) can originate mostly from two processes: (i) photoinduced and microbial assimilations of algae (or cyanobacteria), and (ii) photoinduced and microbial degradation of allochthonous DOM of plant origin and autochthonous DOM of algal/phytoplankton origin (see also chapters "Dissolved Organic Matter in Natural Waters", "Photoinduced and Microbial Degradation of Dissolved Organic Matter in Natural Waters", and "Impacts of Global Warming on Biogeochemical Cycles in Natural Waters"). Small algae can carry out 40–95 % of the bacterivory activity in the euphotic layer of the temperate North Atlantic Ocean in summer, and 37–70 % in the surface waters of the tropical North-East Atlantic Ocean (Zubkov and Tarran 2008). This reveals that the smallest algae have less dependence on dissolved inorganic nutrients (Zubkov and Tarran 2008).

The volume of planktonic bacteria increases as water temperature decreases (Albright and McCrae 1987; Chrzanowski et al. 1988; Bjørnsen et al. 1989), and thus the occurrence of larger cells in the hypolimnion is linked to its low temperature (Wiebe et al. 1992; Callieri et al. 2009; Bertoni et al. 2010). Bacterial cells are often observed to be approximately 30 % larger in the Arctic Ocean and Antarctic coastal waters than in temperate regimes (Straza et al. 2009).

The mechanism behind this size shift is presumably that low temperature in hypolimnion and Arctic or Antactic regions can protect against cell degradation, whereas microbial assimilations of planktonic bacteria cells can release both nutrients and autochthonous DOM. Correspondingly, high temperatures along with solar radiation and surface waters mixing by strong waves are effective in photolytically and microbially releasing nutrients and autochthonous DOM. These two effects could be responsible for the occurrence of large cells in low temperature regions including the hypolimnion. The photoinduced and microbial releases of nutrients, photo-/microbial products, and autochthonous DOM from algae/phytoplankton (Mostofa et al. 2009; Zhang et al. 2009; Tranvik et al. 2009; Zepp et al. 2011; Ma and Green 2004; White et al. 2010; Liu et al. 2010; Mostofa et al. 2005; Bushaw et al. 1996; Molot et al. 2005; Johannessen et al. 2007; Borges et al. 2008; Kujawinski et al. 2009; Lohrenz et al. 2010; Omar et al. 2010; Cai 2011) are responsible for low photosynthesis in most upper surface layers.

It has also been observed that lower photosynthesis in the shallower epilimnion (1 m) than in the deeper epilimnion (3 m) (Nozaki et al. 2002) might be the effect of higher photoinduced degradation of algae near the water surface. This effect, coupled with strong wind mixing and turbulence can decrease the size structure of phytoplankton or algae in the upper epilimnion, thereby decreasing the photosynthetic efficiency (Cermeno et al. 2005; Nozaki et al. 2002). Note that physical mixing in the surface mixing zone is an important factor for promoting the photoinduced degradation of DOM (see chapter "Complexation of Dissolved Organic Matter With Trace Metal Ions in Natural Waters").

5.11 Effects of Global Warming

Global warming causes an increase in water temperature, lengthens the summer season, extends the surface water mixing zone and increases the stability of the vertical stratification in large parts of lakes and oceans. An increase in photoinduced and microbial degradation rates of OM (DOM and POM) by global warming may affect water transparency and generation of photo- and microbial products (H_2O_2, CO_2, DIC, and so on), may modify seasonal patterns in chlorophyll or primary production, contents of nutrients (NO_2^-, NO_3^-, and PO_4^{3-}), carbon cycling, pH values, microbial food web stimulation that varies seasonally on a variety of time scales, and the depth of the mixing layer (see also chapters "Dissolved Organic Matter in Natural Waters", "Chlorophylls and Their Degradation in Nature", and "Impacts of Global Warming on Biogeochemical Cycles in Natural Waters") (Mostofa et al. 2009; Baulch et al. 2005; Morris and Hargreaves 1997; Cooke et al. 2006; Huisman et al. 2006; Malkin et al. 2008; Davis et al. 2009; Castle and Rodgers 2009; Mostofa and Sakugawa 2009; Keeling et al. 2010; Zepp et al. 2011; Granéli et al. 1998). Two phenomena can result from this. First, in water with high contents of OM, photoinduced and microbial processes that correspond to high photosynthesis may be prolonged, thereby causing the prolongation of the primary productivity (Malkin et al. 2008). This may eventually result into toxic or harmful algal bloom in natural waters. Second, low photosynthesis could take place in waters with low contents of OM, causing low production of photo- and microbial products. This can subsequently reduce the vertical mixing and suppress the upward flux of nutrients, leading to a decrease in primary production in oceans (Huisman et al. 2006).

An increase in water temperature by global warming can also decrease the concentration of dissolved oxygen (O_2) in natural waters (Keeling et al. 2010; Epstein et al. 1993; Garcia et al. 1998; Sarmiento et al. 1998; Plattner et al. 2001; Bopp et al. 2002; Keeling and Garcia 2002; Matear and Hirst 2003). This could enhance the growth of cyanobacteria and other algae (Epstein et al. 1993) and/or decrease the growth of other organisms (Keeling et al. 2010). The decrease of dissolved O_2 in the upper surface layer would occur because of decreased O_2 solubility in warmer water and due to photoinduced generation of superoxide radical ion ($O_2^{\bullet -}$) and H_2O_2 (see chapter "Photoinduced and Microbial Generation of Hydrogen Peroxide and Organic Peroxides in Natural Waters" for detailed mechanism) by the effect of global warming. An increase in O_2 can enhance the production of H_2O_2 (Moffett and Zafiriou 1990) and different algae can show unalike responses to O_2 concentration (Pope 1975). This may for instance be linked to eutrophication from excess algal growth. The most prominent symptoms of eutrophication are oxygen depletion in bottom waters and harmful algal blooms (Richardson and Jorgensen 1996).

The decrease of dissolved O_2 in deeper waters would be caused by the decrease in vertical mixing of the water column due to the longer stratification period as a consequence of global warming. This effect can reduce the primary production as well as to survival of organisms in deeper water layers, particularly in lakes and oceans. Earlier studies did not provide any clear mechanisms about the decrease of dissolved O_2, which includes changes in ocean circulation rates (Bindoff and McDougall 2000; Shaffer et al. 2000; Emerson et al. 2001; Keller et al. 2001), in preformed values (Garcia et al. 1998), in Redfield ratios (Pahlow and Riebesell 2000), and in biological production (Emerson et al. 2001). The abundance and geographic distribution of toxin-producing algae is significantly increasing with respect to global warming and because of increased anthropogenic input of nutrients to aquatic environments (Shumway 1990; Harvell et al. 1999; Haines et al. 2000; vanDolah 2000; Shumway et al. 2003; Phlips et al. 2004; Yan and Zhou 2004; Luckas et al. 2005). The effects of global warming on waters are extensively discussed in the global warming chapter, which can help understanding the overall effects on photosynthesis and other key biogeochemical issues (see chapter "Impacts of Global Warming on Biogeochemical Cycles in Natural Waters").

5.11.1 Harmful Algal Blooms

The harmful algal blooms are presumably an effect of global warming on waters with high content of DOM and POM, as extensively discussed in earlier sections. Harmful algal blooms can cause loss of phytoplankton competitor motility, inhibition of photosynthesis, inhibition of enzymes, membrane damage, large fish kills, shellfish poisoning, deaths of livestock and wildlife, death of coral reefs and, finally, illness or even death in humans (Yates and Rogers 2011; Llewellyn 2006; Richardson 2007; Prince et al. 2008; Etheridge 2010; Harvell et al. 1999; Hallock and Schlager 1986; Hallegraeff 1993; Negri et al. 1995; Braun and Pfeiffer 2002; Landsberg 2002; Legrand et al. 2003). Autochthonous organic compounds (e.g. autochthonous fulvic acids) and nutrients are generally produced by algae or phytoplankton, either biologically (also termed allelopathy: a biological phenomenon by which an organism can produce various types of biochemicals, which can influence growth, survival, death, and reproduction of other organisms) or photolytically (see also chapters "Dissolved Organic Matter in Natural Waters", "Photoinduced and Microbial Degradation of Dissolved Organic Matter in Natural Waters", "Colored and Chromophoric Dissolved Organic Matter in Natural Waters" and "Fluorescent Dissolved Organic Matter in Natural Waters" for detailed description) (Mostofa et al. 2009, 2011; Prince et al. 2008; Zhang et al. 2009). In addition, various types of algae such as diatoms, dinoflagellates and cyanobacteria can produce toxins that can cause death of higher organisms (Castle and Rodgers 2009; Falconer 1993). Blooms of a red-tide dinoflagellate such as *Karenia brevis*, occurring in the coastal seawaters, and *Prymnesium parvum*, also known as golden algae, can produce neurotoxic compounds (brevetoxins) that can kill fish and accumulate in shellfish (Yates and Rogers 2011; Landsberg 2002; Southard et al. 2010; Tester et al. 1991). Moreover, autochthonous compounds and toxins produced during toxic algal blooms are susceptible to decrease the photosynthetic efficiency of natural waters.

6 Scope of the Future Researches

The mechanisms of the photosynthetic reaction and the changes of the photosynthetic efficiency of organisms are affected by the different factors discussed in this study. A number of issues may greatly assist to improve the present understanding of photosynthesis. For example, formation of complexes between metal ions and the functional groups of PSII or PSI is a new suggestion about the processes that might occur in aquatic environments. Earlier studies did not place much attention on the complexation theory, which may greatly assist a better understanding of similar researches. The effects of organic matter (DOM and POM) and of other factors on photosynthesis are important for understanding the mechanisms of the release of electrons and O_2, as well as other vital phenomena. The complexation theory may provide a better understanding of the molecular basis for the mechanisms of photosystem tolerance to salt or metal ions stress. If proven, such a theory may greatly help the introduction, by plant breeding and genetic engineering, of salt tolerance in crop plants.

The need for additional studies in photosynthesis can be summarized as follows: (i) Observations are required of the effects of diverse toxic and non-toxic organic substances and metals on efficiency of the photosynthesis of various microorganisms; (ii) The mechanism of relase of O_2 from H_2O_2 during photosynthesis should be substantiated; (iii) Special attention should be paid to the photosystems crystal structure, to find out any presence of H_2O_2 (or O_2) instead of H_2O. Concurrently, further studies are needed that take special attention during sample preparation, to avoid the possible decomposition of H_2O_2. Such studies would help solving the debate concerning the process of oxygen release; (iv) A better understanding is required of the effect on photosynthesis of exogenous H_2O_2, produced from allochthonous DOM (humic substances including fulvic and humic acids); (v) The effect of autochthonous DOM (autochthonous fulvic acids of algal/phytoplankton origin) on photosynthesis also requires better understanding; (vi) Crystal structures of PSI or PSII do not include any information about dissolved O_2, but they are composed of about 1,300 water molecules (Umena et al. 2011) and issue that will need further studies to be clarified. Finally, it is important to remember during the sample processing of any photosynthesis experiments that H_2O_2 is rapidly decomposed microbilly and it is also rapidly produced under light condition.

7 Nomenclature

CCM	Carbon-concentrating mechanism
Chl	Chlorophyll
CO_2	Carbon dioxide
DIC	Dissolved inorganic carbon = dissolved CO_2, H_2CO_3, HCO_3^-, and CO_3^{2-}
DOM	Dissolved organic matter

Ga	Gigaannum: 10^9 years
H_2O	Water
H_2O_2	Hydrogen peroxide
MAAs	Mycosporine-like amino acids
$^1O_2$	Singlet state of oxygen
$^3O_2$	Triplet state of oxygen
$O_2^{\bullet -}$	Superoxide radical anion
OEC	Oxygen-evolving complex
POM	Particulate organic matter
PSI	Photosystem I
PSII	Photosystem II
ROS	Reactive oxygen species
Rubisco	Ribulose Bisphosphate Carboxylase-Oxygenase
UV	Ultraviolet
WOC	Water-oxidizing complex

Problems

1. Define oxygenic photosynthesis and how does it differ from anoxygenic photosynthesis. Explain three key functions of photosynthesis in aquatic environments.
2. Define the key photosynthetic reactions under the hypotheses of H_2O and H_2O_2 involvement.
3. Which and how many Chl molecules can participate in the primary donor sites in PSI and PS II under illumination?
4. Explain the mechanism of H_2O_2 formation from chlorophyll bound in photosynthetic cells and ultrapure water under illumination.
5. Why are PSI and PSII composed of a number of chlorophyll molecules in their structures?
6. Explain the mechanism of electron transfer and O_2 release from PSII during photosynthesis.
7. Distinguish the various factors that influence photosynthesis. How do seasonal light cycle and temperature affect photosynthesis?
8. Why do precipitation/rainfall substantially enhance plant photosynthesis?
9. Explain the mechanism for the occurrence of algal (cyanobacterial) bloom in waters with high contents of DOM and POM. How does global warming accelerate the algal bloom in natural waters?
10. How do trace metal ions become toxic during phytoplankton photosynthesis? Explain the mechanism.
11. Explain how does salinity affect both plant and phytoplankton photosynthesis.
12. How can UV radiation affect phytoplankton photosynthesis?
13. How does metal toxicity impact organisms or induce cancer in humans?

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"*If H_2O would decompose by the reaction with CO_2* in *photosynthesis, then all H_2O would convert into O_2 by organisms and plants after the origin of life on earth to date and no H_2O would remain in the biosphere.*

Instead of H_2*O, photoinduced generation of H_2O_2 from dissolved O_2 in water bound in photosynthetic cells is reacted with CO_2 in photosynthesis that can limit the photosynthesis under light condition.*

Then further conversion of H_2O_2 *to O_2 either through photosynthesis [$xCO_{2(H2O)} + yH_2O_{2(H2O)} \rightarrow C_x(H_2O)_y + O_2 + E$ (±)] or both photolytically ($2H_2O_2 + h\upsilon \rightarrow O_2$ + unknown oxidant) and biologically ($2H_2O_2$ + catalases/peroxidases $\rightarrow O_2 + 2H_2O$) may balance the environment."*