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The Enhancement of Photosynthesis by Fluctuating Light

David Iluz[1,2], Irit Alexandrovich[1] and Zvy Dubinsky[1]
*[1]The Mina and Everard Goodman Faculty of Life Sciences,
Bar-Ilan University, Ramat-Gan
[2]The Department of Geography and Environment, Bar-Ilan University, Ramat-Gan,
Israel*

1. Introduction

As early as 1953, reports documenting the enhancement of photosynthesis by plants when exposed to flashing light, as compared to the same photon dose under continuous light, were published (Kok, 1953; Myers, 1953). Using the unicellular green alga *Chlorella,* the effects of varying frequencies and dark/light duration ratios on photosynthetic rates were described. Such results have kindled research on their role in nature and their application in various photobioreactors and algal mass culture facilities, aimed at the production of valuable carotenoids, lipids, and additional products of commercial interest, such as biodiesel. The present review discusses the characteristics of the fluctuating underwater light field in natural waters, bioreactors, and ponds, and summarizes their effects on photosynthesis and growth.

Based on the advances in the understanding of the various mechanisms and processes affecting the efficiency and yields of photosynthesis, we discuss their interaction with continuous and intermittent light. The following are examined:

a. Post-illumination enhanced respiration
b. Photodynamic damage to the 32kd protein of Photosystem II (PSII)
c. The xanthophyll cycle
d. Thermal-energy dissipation
e. In addition, the enhancement phenomenon is examined in relation to the intensity of the ambient light

In the context of the present review, it is appropriate to list and compare the different terms and definitions used in the description and study of fluctuating light fields (Table 1). In the following review, the term 'fluctuating light' is used for clarity and consistency.

1.2 Fluctuating light in terrestrial ecosystems
1.2.1 Canopy

In many forests with closed canopies, only a small fraction (0.5-5%) of the solar radiation incident above the canopy reaches the understory. Understory plants in these forests experience a highly dynamic light environment, with brief, often unpredictable periods of direct solar irradiance (sunflecks), punctuating the dim and diffuse background irradiance.

These sunflecks are combined with diurnal fluctuations in irradiance, ranging from sunflecks lasting only a few seconds or less in heavily shaded sites to cloud-induced fluctuations ("shadeflecks") lasting up to an hour or longer in open sites (Knapp & Smith, 1987). The nature of sunflecks, their size, shape, duration, and peak photon flux density depends on the height and precise arrangement of vegetation within the forest canopy as well as the position of the sun in the sky. The occurrence of a sunfleck at a particular location and time in the forest understory depends on different, often interacting, factors: the coincidence of the solar path with a canopy opening; the movement of clouds that obscure or reveal the sun; and the wind-induced movement of foliage and branches (in the canopy or in the understory plants themselves). These factors interact to yield a highly dynamic light environment in which the photon flux reaching leaves can increase or decrease over orders of magnitude in a matter of seconds. The effects of sunflecks on understory photosynthesis were studied in several works and revealed conflicting results (Leakey et al., 2002, 2005). In some cases, photosynthesis as CO_2 assimilation by understory seedlings was enhanced, whereas at elevated temperatures (38°C), it decreased.

Subject	Condition	Frequency	Organism	Reference
Sunflecks	Caused by leaf movement in forest understory	Seconds to minutes	Dipterocarp seedlings	Leakey et al. (2002, 2005)
Flickering light	Underwater high-frequency light fluctuation resulting from lens effect on the water surface	High frequency Less than one second	endosymbiont photosynthesis of reef-building corals	Yamasaki and Nakamura (2008); Veal et al. (2010)
Fluctuating light	Sunlight focusing by short sea-surface waves; appears in peculiar form of irradiance pulses, termed 'flashes'	At depth of 1 m, up to 200 min^{-1}	Reef-building coral *Acropora digitifera*	Stramski (1986)
Intermittent light	Short flashes	In values of a few milliseconds. The critical flash time is a function of the incident intensity. The dark time must be 10 times as long as the flash time	*Chlorella pyrenoidosa* cultures	Kok (1953)
Flashing light		In photobioreactors, known as 'flashing light effect'		Myers (1953)

Table 1. Some historical observations of fluctuating light on the water surface and underwater

1.2.2 In the aquatic environment

In natural aquatic systems, there are several factors that cause variations in irradiance. Irregular variations are caused by surface wave movement (Walsh & Legendre, 1983), cloud cover (Marra & Heinemann, 1982), and the vertical movement of phytoplankton (Falkowski & Wirick, 1981).

The high-frequency (less than 1 Hz) light fluctuations, known as 'flicker light', are produced by a lens effect of moving water surface, or waves, that simultaneously focuses and diffuses sunlight in the few upper meters (Hieronymi & Macke, 2010) (Fig. 1a). Because flicker light potentially produces excessively strong light as well as dimmer light, such fluctuations may have profound effects on the photosynthesis of benthic algae, seagrasses, and zooxanthellate corals. We will limit our discussion to shallow-water sessile organisms that are particularly prone to be influenced by a recurrent light provision anomaly such as these flickers. The effect diminishes with depth due to the shape- and hence the focal length of waves and scattering by particles (Fig. 1).

Waves act as lenses because of the differences in refractive indices between air and water, focusing light below the wave for a brief period. In shallow water, this effect can be seen clearly by eye (Fig. 1), appearing against a dark background as flickering bands of focused light. The location of the focusing events depends upon the shape of the waves. Large, rounded waves focus into deeper regions than small, sharply curved ripple waves (Kirk, 1994; Schubert et al., 2001) (Fig. 1).
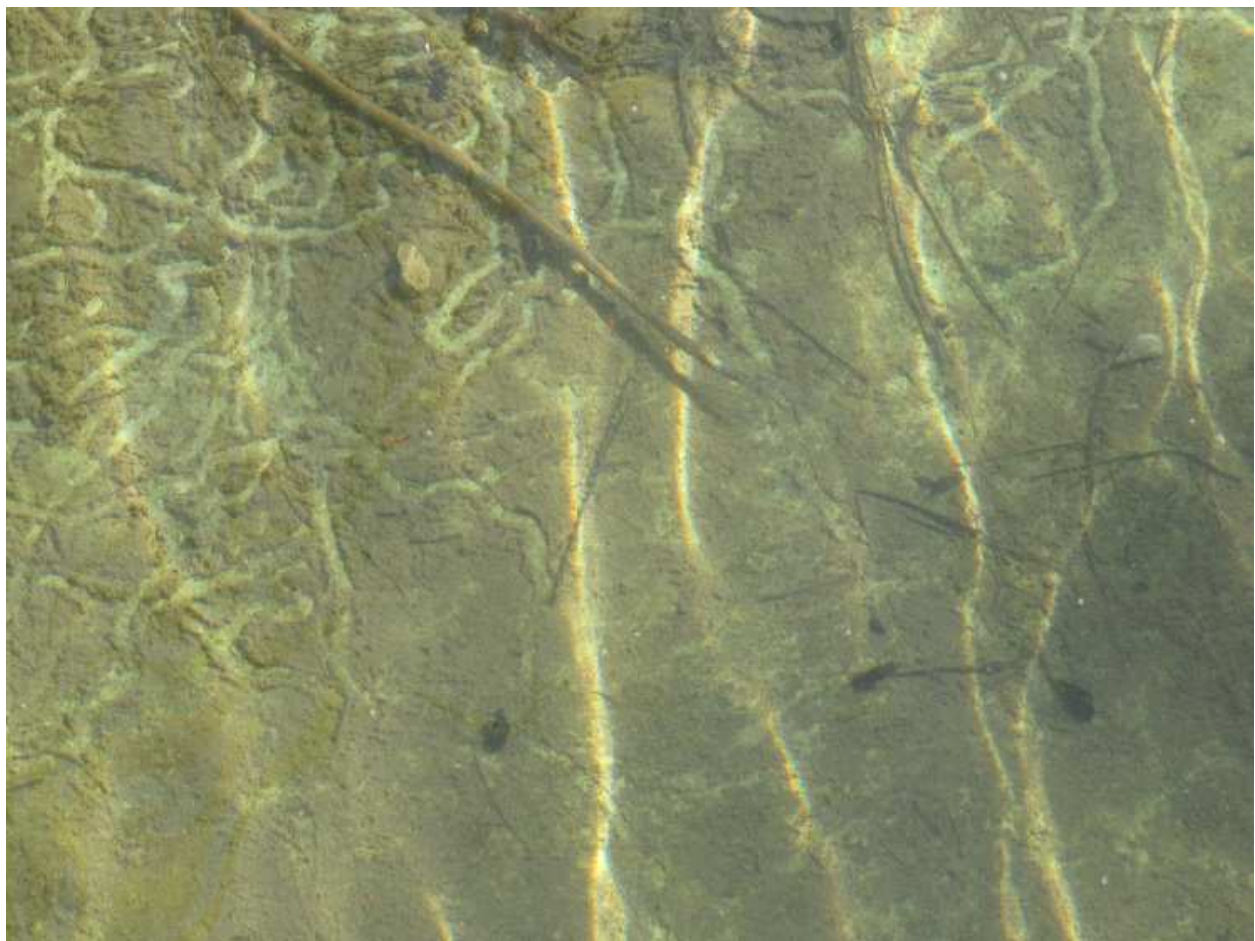

Fig. 1. Underwater light patterns on a shallow sandy bottom due to surface waves

Underwater irradiance fluctuations result from temporal, non-linear variations of sea-surface topography. When solar radiation is broken, the intensity and light penetration depth depend on the wavelength of light and general and local water features. Phytoplankton, which live at different depths, must adjust and be acclimated to the features of the underwater field to which they are exposed for doing photosynthesis (Kirk, 1994).

Ripples on the water surface cause considerable heterogeneity of subsurface light (Figs. 2, 3) through the lens effect, which simultaneously focuses and diffuses sunlight in the upper few meters, producing a constantly moving pattern of interspersed light and shadows on the substrate. Due to that effect, light intensity in shallow water environments sometimes reaches more than 9,000 µmol quanta $m^{-2}s^{-1}$, corresponding to 300-500% of the surface light intensity (Fig. 1) (Schubert et al., 2001). The lens effect produced by waves generates narrow belts of supersaturating light that pass over the bottom surface for less than a second (Figs. 2, 3). In addition to the focusing effect of light, the same curvature of the water surface also produces lower light intensity intervals interspersed between the intense peaks, namely, producing a light-diffusing effect (Schubert et al., 2001). This light-diffusing effect may serve as a relaxation period for algal photosynthesis.
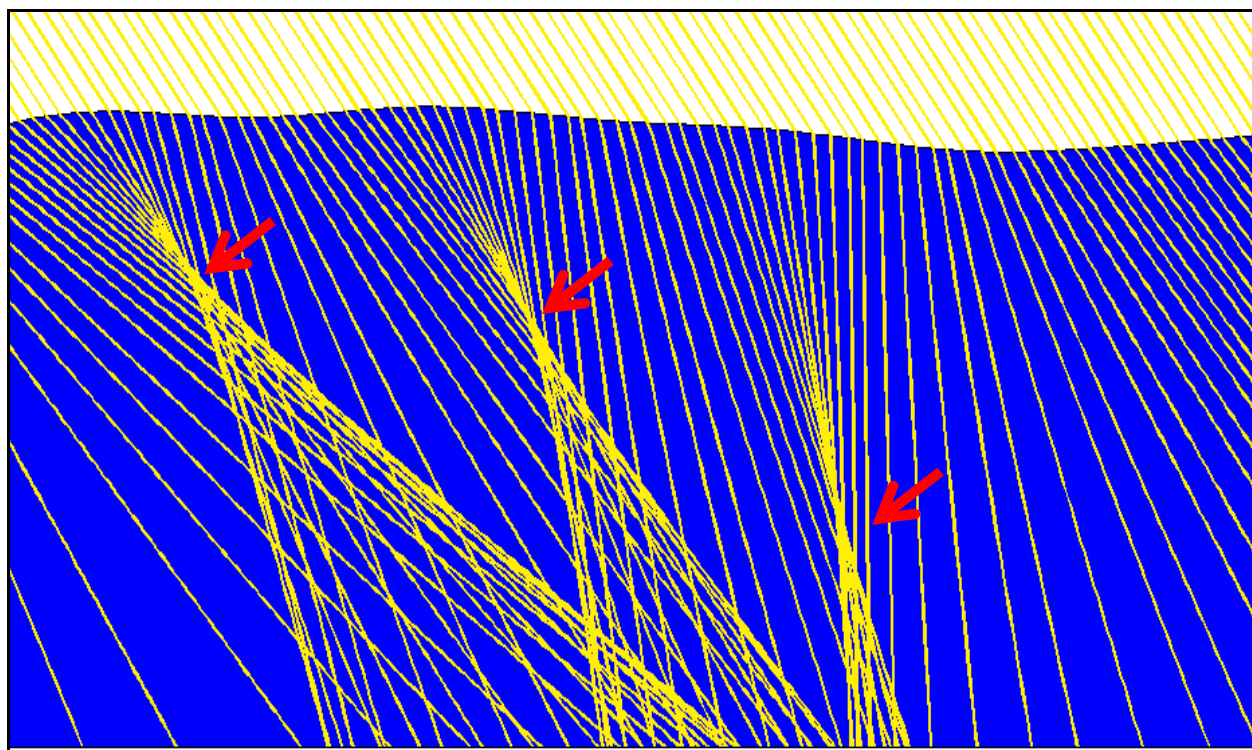

Fig. 2. Focusing beams beneath wave crests and scattering under troughs. The arrows indicate the dependence of maximal-effect depth on wave radius (after Grosser et al., 2008).
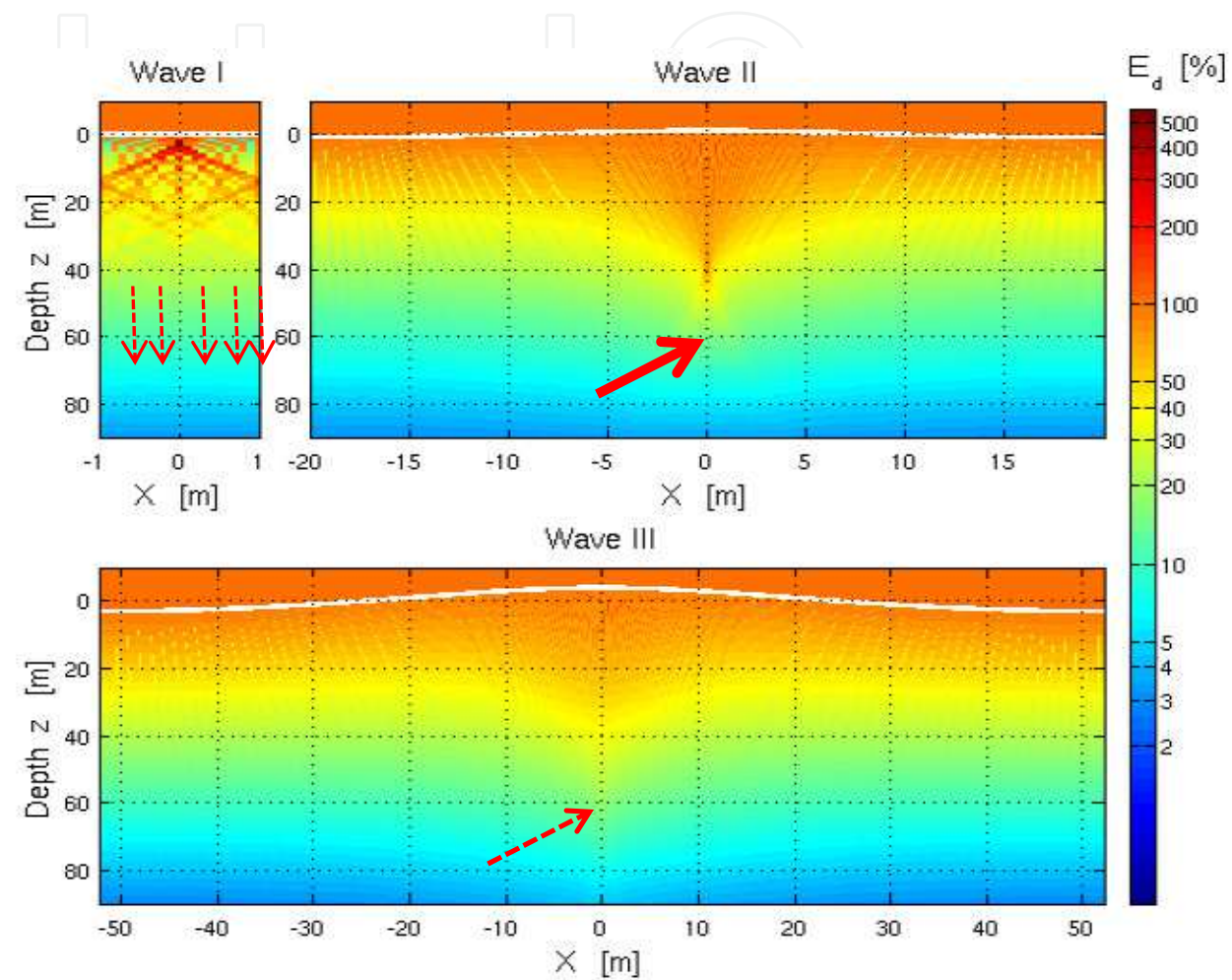
Fig. 3. Downward irradiance patterns below three waves with respect to 100% at the surface (note the logarithmic color scale and the different scales of the x axes) Wave I, flat surface, no lensing; Wave II, strong lensing; wave III, large radius, weak lensing (after Hieronymi and Macke (2010)).

Due to its dependence on wave geometry and on their horizontal movement, there is a tight coupling between wind velocity, wave height, surface smoothness and the underwater light field (Fig. 4). The effect of small-scale roughness on preventing wave lensing was applied in the study by Veal et al. (2010), who used water sprinklers to obtain non-lensing controls.
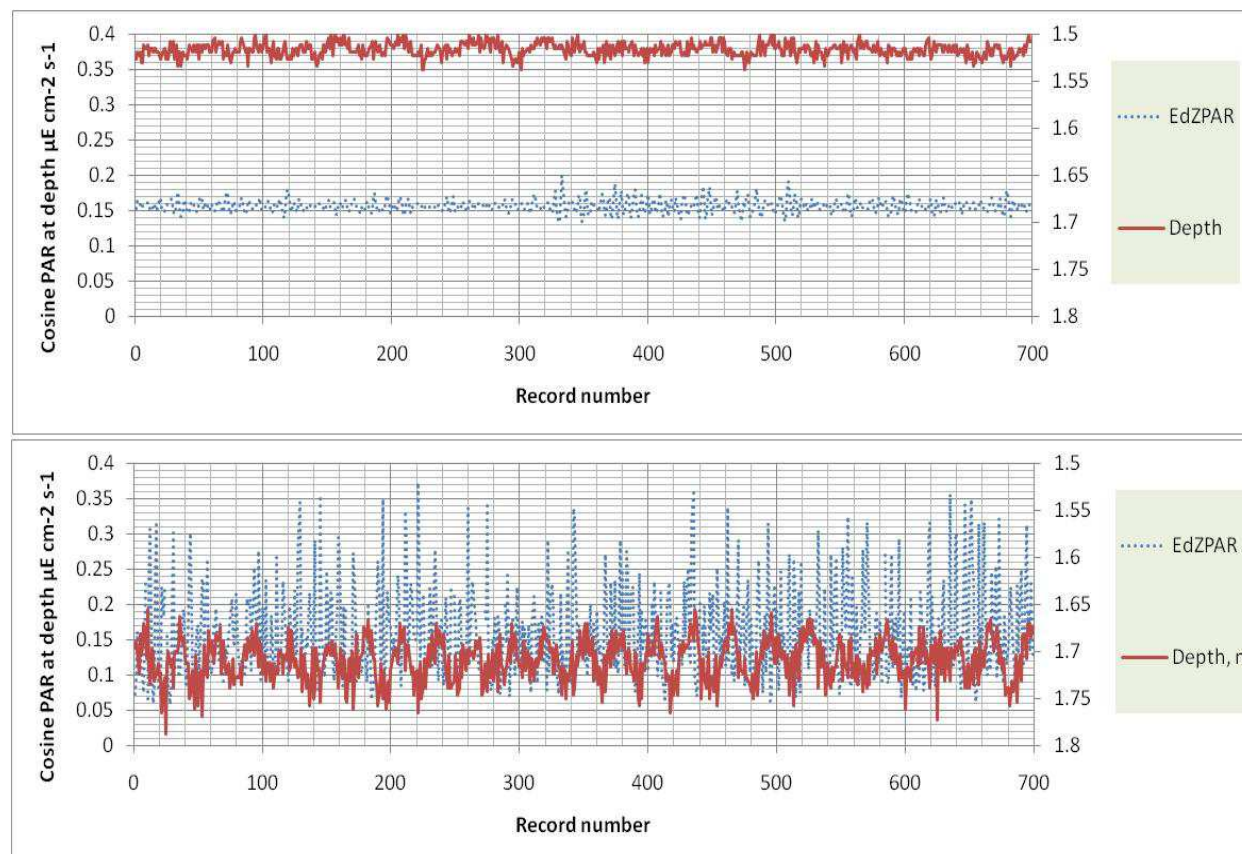
Fig. 4. PAR fluctuations as measured by PRR800 at 0.8 m depth: A) on a very calm day (0.4 m/sec wind); and B) on a windy day (7 m/sec wind). The depth values are not calibrated but do represent the amplitude of surface waves as sensed by the pressure sensor of the PRR800 unit. Data were recorded at 15 Hz without any shading effect, downwind of the IUI pier, in the gulf of Eilat. Coefficient of variance=40% (Dishon, personal communication)

1.3 Applications in bioreactors and cultures

Microalgal biotechnology is one of the emerging fields in our era. In recent years, there has been great interest in using microalgae as sources of a wide range of fine chemicals, oils, and polysaccharides (Borowitzka, 1992; Jensen, 1993; Munro et al., 1999). Many laboratory scale photobioreactors have been reported but most of them are extremely difficult to scale up due to the phenomenon of mutual shading at high cell densities. Light, which is an essential factor in the phototrophic growth of microalgae, cannot be stored, so it must be supplied continuously. Due to the high light-harvesting efficiency of chlorophyll in microalgae, algae absorb all the light that reaches them even though they cannot use all the photons. This phenomenon causes a dramatic decrease in light utilization efficiency since the photons cannot penetrate into the depth of the culture, even when enough photons are supplied at the surface. Many photobioreactors have been developed to overcome this problem (Park & Lee, 2000; Qiang & Richmond, 1996; Richmond et al., 2003).

Much recent research effort has been devoted to finding a means for shifting the group of cells exposed to the light in such a manner that each cell will receive just its quanta of light and then will immediately be replaced by another one, so that none of the light will be wasted (Richmond, 2004). As the algal cells are propelled by the mixing of the culture

between the surface of the pond, the transparent wall of the reactor, or the dark depth of the culture, the cells are exposed to a fluctuating light regime whose properties depend on the light source and its intensity, spectral distribution and beam geometry, culture density and depth, reactor architecture, and the hydrodynamics of mixing. These parameters define the range of light intensities to which the cells are exposed, as well as their frequency.

There are two major types of photobioreactors that are considered the most common production systems: outdoor open ponds (Fig. 5) and enclosed photobioreactors (Fig. 6). Open ponds have been the most widely used system for large-scale outdoor microalgae cultivation for food and medicine supplements during the last few decades (Borowitzka, 1993). They were built as a single unit or multiple joint units, with agitation by means of paddlewheels, propellers, or airlift pumps.
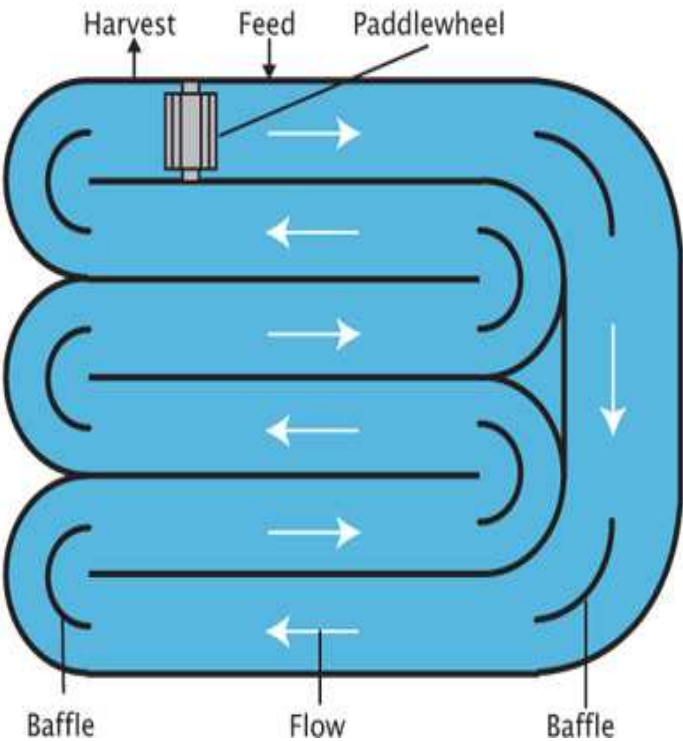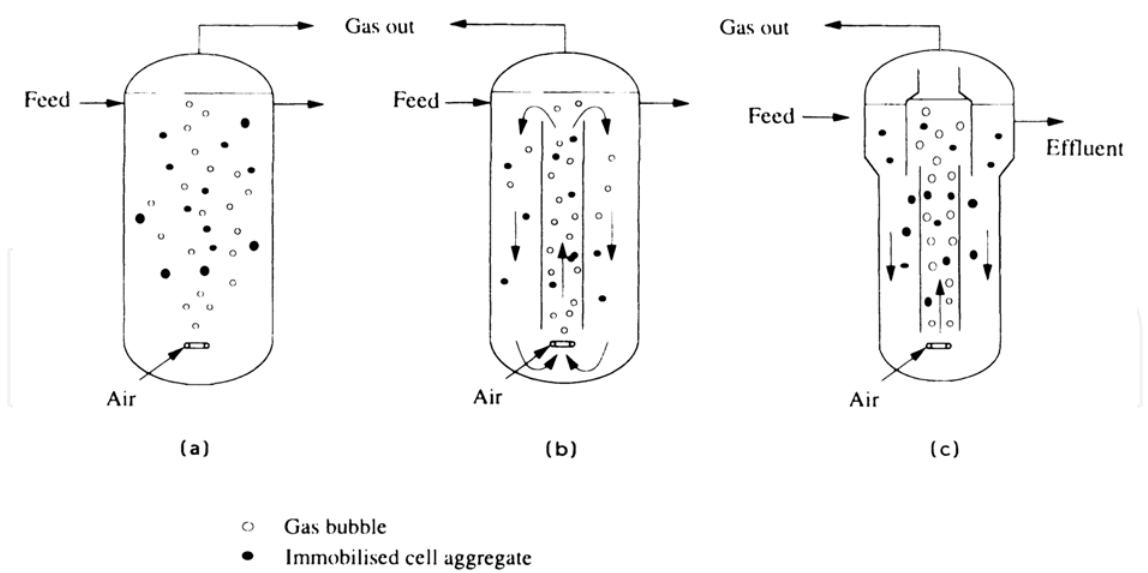

Fig. 5. Open ponds

Fig. 6. Tubular photobioreactors (*left: Cal Poly CEA Energy Working Group,* right:
http://userwww.sfsu.edu/~art511_h/emerging10/natasha/domef/project1algae.html)

Due to the susceptibility of open pond systems to contamination by opportunistic algal species, enclosed photobioreactors have evolved. Two major types of enclosed photobioreactors are tubular and plate types. Due to the enclosed structure and relatively controllable environment, enclosed photobioreactors can reach high cell densities and easy-to-maintain monoculture (Lee, 2001; Ugwu et al., 2008). Tubular photobioreactors (PBRs), constructed of transparent glass or plastic, is one of the popular outdoor systems for mass algae cultivation. It can be horizontal, vertical, conical, and inclined in shape. By mixing, it can be an airlift or pump system (Ugwu et al., 2008). The advantages of tubular and plate types of PBR are a narrow light path (1.2-12.3 cm) that allows much higher cell concentration than in the open pond system, a larger illuminating area, and fewer contamination issues.

Both the spectral quality and the intensity of light are important for algal growth and metabolism. In high-density algal cultures, the light delivery becomes restricted as the cell concentration increases. This mutual shading or self-shading will shield the cells that are apart from the illumination surface from receiving light. As a result, the light penetration depth should be calculated in order to achieve a successful photobioreactor (Lee, 1999).

One of the solutions was to create a turbulent flow by installing static mixers. Turbulent-flow conduction in the reactor exposes the cells at short intervals to high light intensities at the reactor surface and they can, therefore, process the light energy collected in the subsequent dark phases.

A further way of generating turbulence in the photobioreactor is to provide a gassing device that achieves the desired effect at an appropriate gassing rate. The provision of flow-conducting intervals can also improve the flashing-light effect if a defined frequency is established for the illumination time (6509188, 2001)

The flashing light effect should be considered because turbulent flow in the reactor gives microalgae a chance to come close to the irradiated surface in the opaque medium at an irregular frequency, and this intermittent illumination enhances photosynthesis of the algae (Sato et al., 2010).

In high cell-density culture, a light gradient inside the photobioreactor will always occur due to light absorption and mutual shading by the cells. Depending on the mixing characteristics of the system, the cells will circulate between the light and dark zones of the reactor. The main limiting factor for the development of microalgal biotechnology is that light energy cannot be stored and homogenized inside the reactor. In photobioreactors, the light regime is determined by the light gradient and liquid-circulation time. Strong light can be efficiently used by working at the optimal cell density in combination with a proper liquid-circulation time (Richmond, 2000).

The increase in turbulence distributes the light optimally in the reactor chamber of the photobioreactor. Operation as an airlift loop ensures high turbulence with low sharing forces acting on the algal cells. Given high turbulence and, at the same time, high radiation intensity, the flashing-light effect can be utilized, and the cells would not have to be continuously illuminated (Fig. 7) (Patent 6509188, 2001).

The principle of the airlift loop reactor is that it achieves optimal light supply due to a low layer thickness and the directed conduction of flow in the reactor via static mixers. The solution lies in directed transportation of the cells, which is forced by the installation of the static mixers: the rising gas bubbles are diverted to the static mixes and set the culture

medium flowing in a stationary, circular current. The algal cells are, thereby, transported to the light and then back into the shaded zone at a rhythm of approximately 1 Hz. The average light intensity, which is evenly distributed onto all algal cells in the reactor, can be varied by changing the spacing between the reactors outdoors (Fig. 8) (Patent 6509188, 2001).
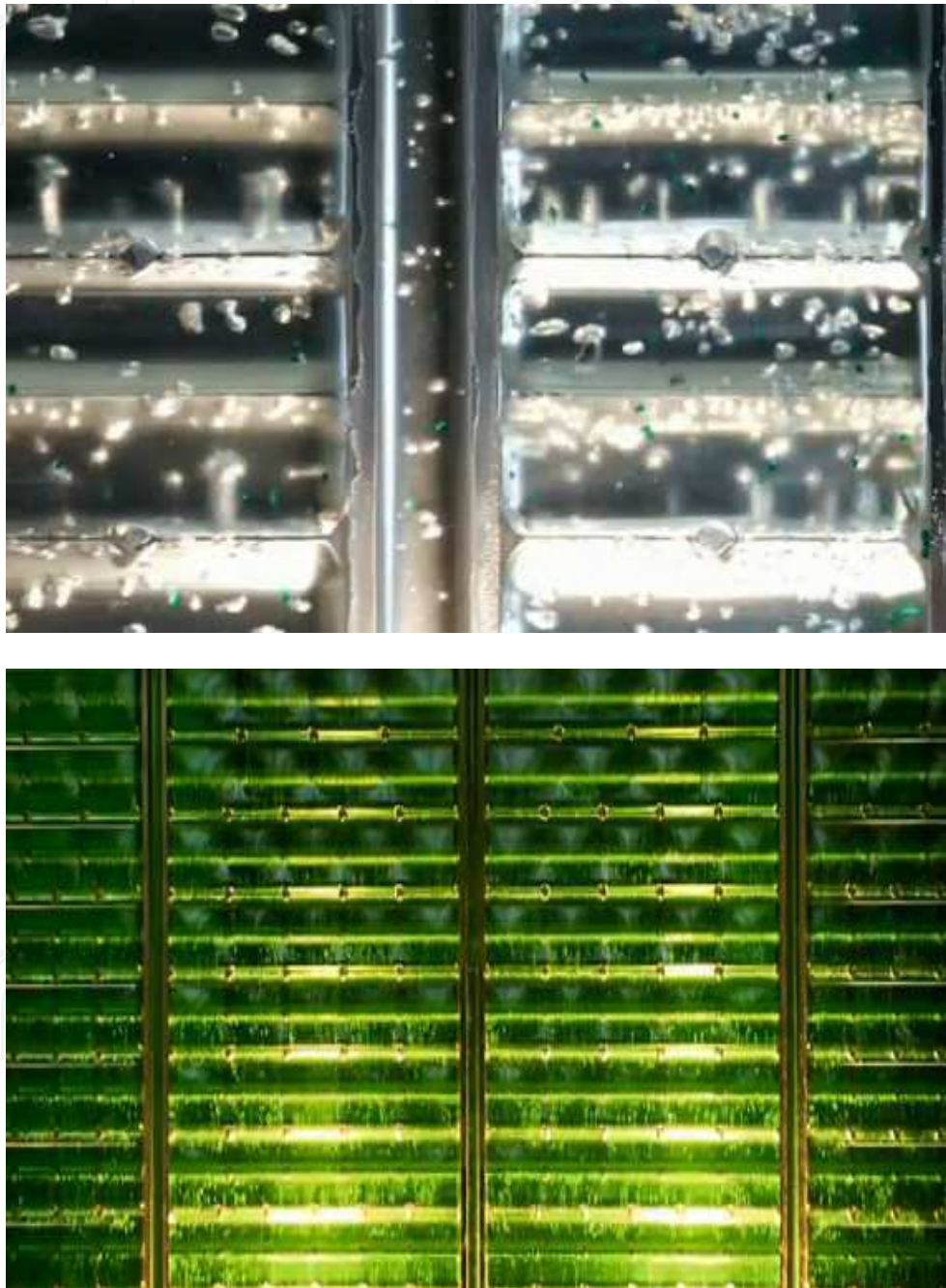

Fig. 7. Flat-panel airlift (FPA) reactor with static mixers for defined transport of algae to the light. Up) Fraunhofer Institute for Interfacial Engineering and Biotechnology; and Down) Subitec - Sustainable Biotechnology
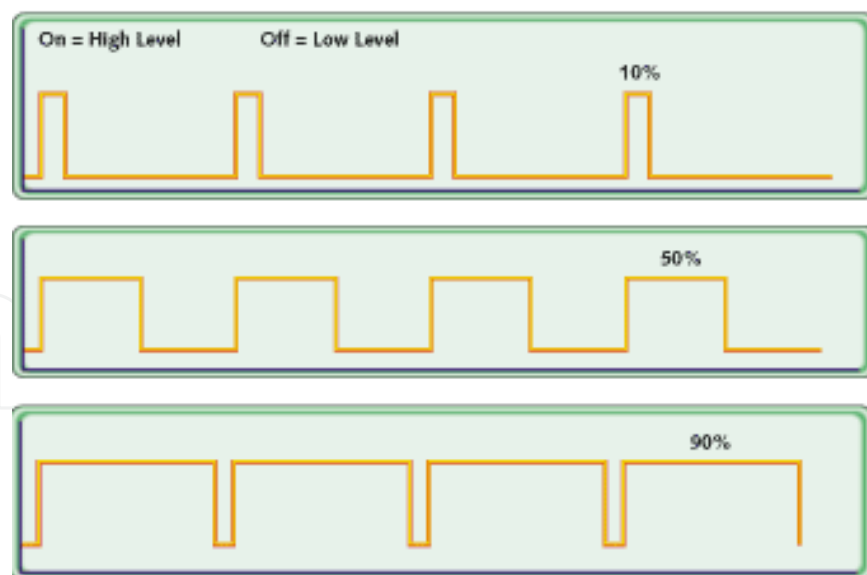
Fig. 8. The duty cycle indicates the 'on' or 'off' time in percent, ranging from 0% to 100% of period for repetitive pulse train. The duty cycle is the proportion of time in which the pulse is 'on', and is expressed as a percentage: duty cycle = 100% * (pulse time high)/(total pulse period).(http://www.dprg.org/tutorials/2005-11a/index.html)

1.4 The enhancement of photosynthesis by fluctuating light

Reports documenting the enhancement of algal photosynthesis when exposed to flashing light, described the effects of varying frequencies and dark/light duration ratios (Kok, 1953; Myers, 1953). These authors had shown that short flashes of high intensity can be used by single celled algae with high efficiency - if separated by sufficiently long dark periods. Kok (1953) has shown that for *Chlorella pyrenoidosa*, the dark time must be at least ten times as long as the flash time for fully efficient utilization of the incident light in photosynthesis. This means that if an algal cell is exposed to high-intensity light for a short time, it can absorb all that light in the 'light' stage of photosynthesis and then utilize it in succeeding stages in the dark. Contrary to the above, Grobbelaar et al. (1996) reported that a longer dark period relative to the preceding light period does not necessary lead to higher photosynthetic rates/efficiencies. He showed that the effect of altering the L/D (Light/Dark) ratio was clearly evident, where at any given L/D frequency the highest photosynthetic rates were measured at a ratio of 1L/1D.

Light/dark cycles have been proven to determine the light efficiency and productivity of photobioreactors. Very fast alternations between high light intensities and darkness (from less than 40 μs to 1 s) can greatly enhance photosynthetic efficiency (Kok, 1953; Matthijs et al., 1996; Nedbal et al., 1996; Phillips & Myers, 1954; Terry, 1986).

Such results have kindled research on their application in various photobioreactors and algal mass culture facilities aimed at the production of valuable carotenoids, lipids, and additional products of commercial interest, such as biodiesel and hydrogen (Grobbelaar et al., 1996; Park et al., 2000; Terry, 1986; Yoshimoto et al., 2005).

Several mechanisms were postulated to explain the enhancement effects of flashing light on photosynthesis. It has been suggested that at high frequencies, there are non-linear effects related to the limited availability of quinone pool receptors under continuous high light (Kok et al., 1970), whereas other works hypothesized Rubisco particle circulation in

turbulent flow (Yoshimoto et al., 2005), and mutual shading of algal cells thereby increasing the time they are exposed to optimal light (Park et al., 2000).

The enhancement of photosynthesis by flashing light (both the rate and the efficiency) has been known for many years. Richmond and Vonshak (1978) and Laws et al. (1983) reported increased growth rates when the stirring speeds of their mass cultures were doubled. They ascribed the increase to a more favorable dark/light cycle with increase turbulence. According to Terry (1986), relatively high photon flux densities are necessary for the enhancement of photosynthesis in a modulating light field.

Furthermore, according to the findings of Grobbelaar et al. (1996), the enhancement of photosynthesis in L/D environments depends on a number of conditions, the most important being that the L/D cycle be less than 1 Hz. Under such conditions, photosynthetic rates and light utilization efficiencies are increased. The prime conclusion of this study was that the photosynthetic rates enhanced exponentially with increasing light/dark frequencies.

Kübler and Raven (1996) studied the enhancement of photosynthesis under fluctuating light simulating marine shallow water conditions in the rhodophytes *Palmaria palmata* and *Lomentaria articulate*. They determined the dependence of the enhancement on flash frequency.

Pons and Pearcy (1992) studied the enhancement of photosynthesis on leaves of soybean plants exposed to constant and flashing light regimes with light flecks of different frequencies, durations, and photon flux density (PFD). The net CO_2 fixation from 1 s duration of light flecks was 1-3 times higher than predicted from steady-state measurements in constant light at the light-fleck and background PFD. This light-fleck utilization efficiency (LUE) was somewhat higher at a high than at a low frequency of 1 s light flecks. LUE in flashing light with very short light flecks (0-2 s) and single 1 s light flecks was as high as 2, but decreased sharply with increasing duration of light flecks.

1.5 Zooxanthellate corals

In a coral endosymbiont exposed to supersaturating light intensities at flicker light conditions, reduced photoinhibition was recorded compared with exposure to constant light of the same supersaturating intensity. Reduction in photoinhibition by flicker light was reported to be more pronounced at high water temperatures in a study on the zooxanthellate coral *Acropora digitifera* (Yamasaki & Nakamura, 2008). Veal et al. (2010) studied the effects of wave lensing on two Red Sea zooxanthellate corals at ambient (27°C) and elevated (31°C) temperatures. They used water sprinklers that broke the water surface, thereby eliminating the lensing effect while having minimal effect on downwelling PAR and UV. In their experiments, they did not find any biological effect of the intense light flashes caused by lensing, and concluded that these flashes do not contribute to the triggering of bleaching episodes.

Regular variations are due to the circulatory motion within internal waves (Savidge, 1986). Regularly fluctuating irradiance has been shown to alter the rate of photosynthesis of marine algae (Savidge, 1986). Enhancement of photosynthesis to values as high as 180% of control have occasionally been recorded (Jewson & Wood, 1975; Marra, 1978). At supersaturating light intensities, photosynthesis was less inhibited by flicker light than by constant light in the reef-building coral *Acropora digitifera* (Yamasaki & Nakamura, 2008).

The effect of light acclimation on the P/I curve is shown in Figure 9: the open arrows show the direction of the response to high light and the solid arrows show the response to low light acclimation. At high light P_{max} increases, while at low light it decreases. Alpha (α) increases with low light acclimation and decreases under high light exposure. The onset of photoinhibition occurs at lower light intensities for low light-acclimated algae compared to high light-acclimated algae that can tolerate much higher light intensities. I_k is lower for low light-acclimated algae than for high light-acclimated algae. Even dark respiration (R_d) varies considerably depending on the light history (Grobbelaar & Soeder, 1985), where high light-acclimated algae will have higher dark respiration rates than low light-acclimated ones. However, the question of the effect of flashing light on the photoacclimation process has not been studied. It remains to be seen whether algae exposed to flashing or fluctuating light acclimate to the peak intensity or to some intermediate value. In Figure 10, the effect of flashing light frequency and intensity on the photosynthesis versus energy relationship is shown. In all cases, a 1/1 light/dark duty cycle was used.
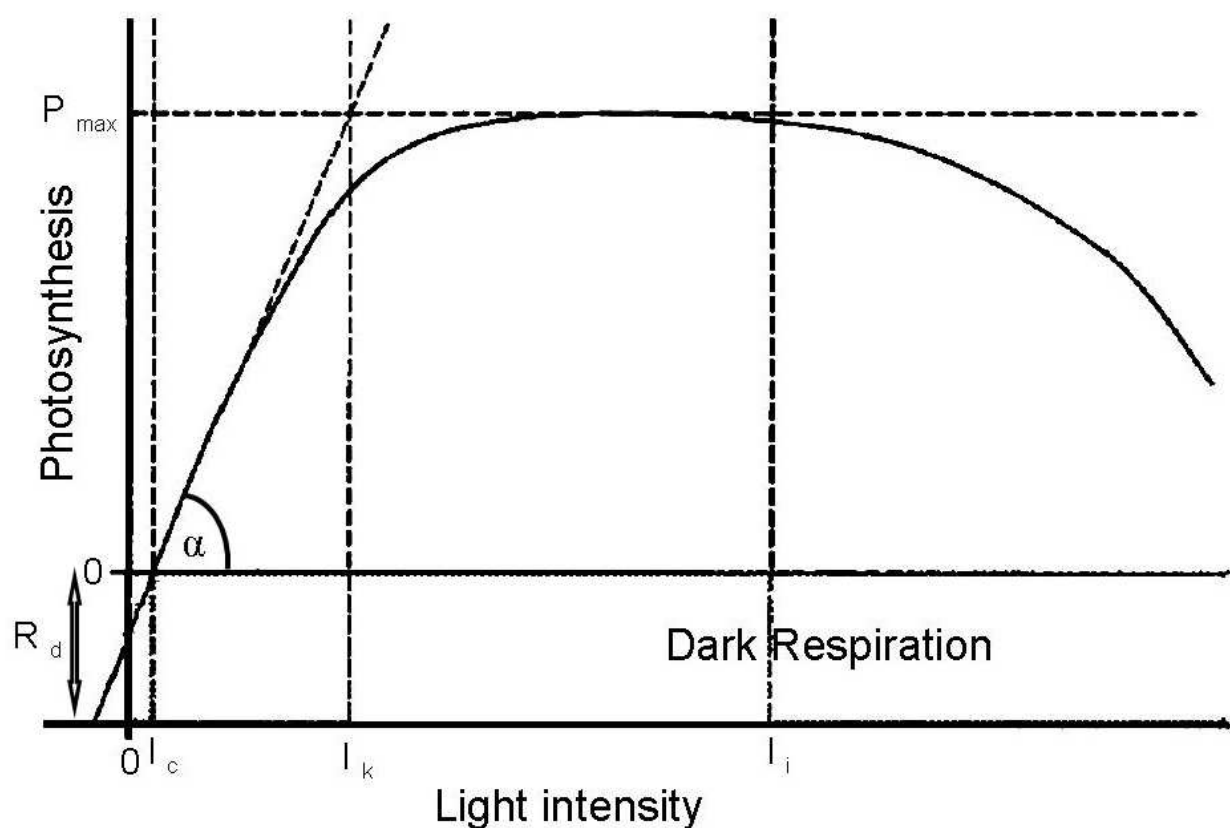

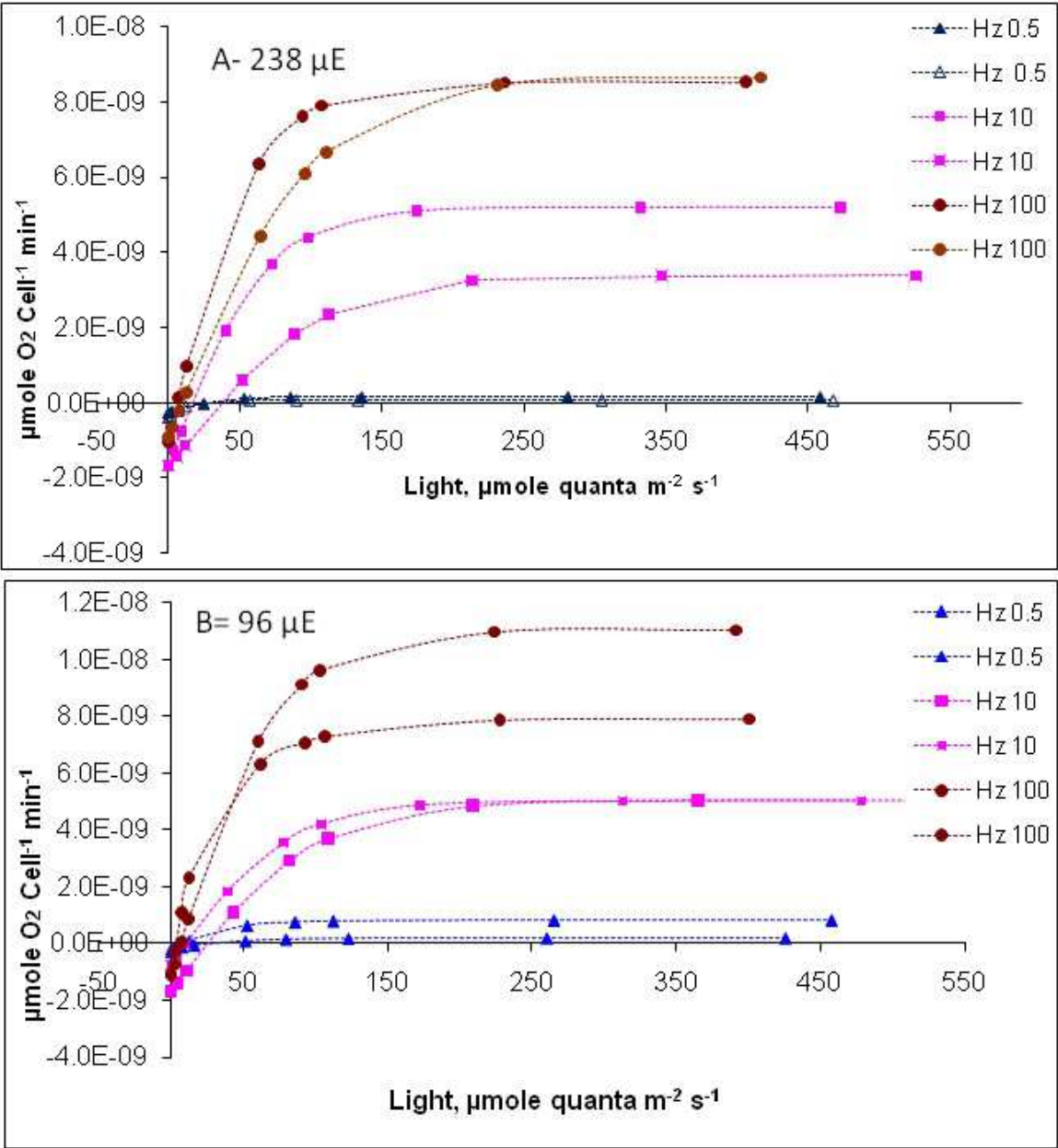Fig. 9. Light-response curve of photosynthesis versus light intensity (Grobbelaar, 2006).

Fig. 10. Photosynthetic rates of the green microalga *Chlorella* sp. subjected to increasing frequencies of light in relation to constant light. Following two weeks of growth, measurements were made at each frequency, two replicates = algae at high light intensity (238 μmole quanta m^{-2} s^{-1}) (A), and B = algae at low light intensity (96 μmole quanta m^{-2} s^{-1}).

1.5.1 The effect on zooxanthellate corals

Effects of flicker light on endosymbiont photosynthesis of the reef-building coral *Acropora digitifera* (Dana, 1846) were evaluated with pulse amplitude modulation chlorophyll fluorometry. At supersaturating light intensities, photosynthesis was less inhibited by flicker light than by constant light. Reduction in photoinhibition by flicker light was pronounced at high water temperatures. Flicker light may strongly influence endosymbiont photosynthesis of corals inhabiting shallow reef habitats, especially during periods of strong solar irradiance and high water temperature.

1.6 Mechanisms

Since fluctuating light enhancement has been observed only under high light intensities, we offer the following putative explanations to that phenomenon. Under high light conditions, photosynthetic organisms recruit several processes to deal with excessive absorbed light and reduce oxidative damage. In terms of energy efficiency, these processes are responsible for losses in photosynthetic production.

These processes are:

a. Photoacclimation - Plants must maintain balance between the energy derived from the light reactions in the chloroplast and the amount of energy utilized during carbon fixation and other metabolic processes. Changes in environmental conditions upset this balance, requiring algae to physiologically adjust, or acclimate (Hüner et al., 1998). In the natural environment, there are daily and seasonal changes in light intensity, creating stress that induces a physiological response (photoacclimation) to optimize growth. Such responses minimize damages stemming from super-optimal intensities, while maximizing light harvesting and quantum yields under dim light. For instance, an increase in light intensity can generate damaging reactive oxygen intermediates that may induce photoinhibition and limit growth (Osmond, 1994). Conversely, when light intensity decreases, cells are unable to generate enough energy via photosynthesis to fulfill their metabolic requirements, again limiting primary production (Falkowski & LaRoche, 1991). Short-term (seconds to minutes) photoacclimation includes the dissipation of excess light energy via the xanthophyll-cycle carotenoids (Demmig-Adams & Adams, 1996) and/or state transitions that can change the excitation energy distribution between photosystems I and II (PSI, PSII) (Bennett, 1983; Bonaventura & Myers, 1969). Long-term photoacclimation (hours) occurs when the short-term changes are insufficient for coping with the changes in light intensity, thus resorting to extensive changes in enzyme activity and gene expression that lead to alterations in the concentration of photosynthetic complexes, leading to changes in antenna composition and photosystem stoichiometry (Anderson et al., 1995; Falkowski & LaRoche, 1991). High light-acclimated cells typically have less photosynthetic units or smaller antennae if photosystem-unit (PSU) numbers remain unchanged, lower cellular content of chlorophylls and other light-harvesting pigments such as fucoxanthin and peridinin, and high concentrations of photoprotective ones, like ꞵ-carotene and astaxanthin. The opposite is true for cells exposed to low light intensities. Overall, photoacclimation attempts to maintain constant photosynthetic efficiency under a variety of light intensities by adjusting the capacity of the plant to harvest and utilize light (Chow et al., 1990). The question is: to what irradiance level do cells acclimate under fluctuating light.

b. Photoinhibition (see Powles, 1984; Lidholm et al., 1987; Long et al., 1994). This process results in a significant loss of photosynthetic production. It involves degradation of the 32-kD D1 polypeptide (e.g., Adir et al. 2003), as well as PSI-A, PSI-B, and acceptor-side–located small photosystem I polypeptides (Tjus et al., 1999). Its extent and kinetics depend on the previous light-history of the organism, and the intensity and duration of the photoinhibitory illumination. We assume that under suitable frequencies, photoinhibition is reduced either since exposure to the high light is too short to bring about damage or that the subsequent dark interval allows for damage repair.

c. Enhanced post-illumination respiration (EPIR) was first reported by Falkowski et al. (1985) and reexamined by Beardall et al. (1994). However, since that phenomenon that by steeply increasing respiration losses reduces net production and yields is dose dependent, the brevity of the high light exposure minimizes its effects.

d. Thermal dissipation, also termed NPQ (nonphotochemical quenching [of fluorescence]) in variable fluorescence-based studies, may account for the loss of from one half to nearly all of the absorbed light energy. Thermal dissipation, measured directly by photoacoustics, depends on the light history of the organism, with losses increasing under high light, and any stress may account for losses of 30-80% of absorbed light energy (Dubinsky et al., 1998; Pinchasov et al., 2005).

e. The xanthophyll cycle allows the fine tuning of the photosynthetic apparatus to ambient light by switching between two states of the pigment couples constituting the xanthophyll cycle. When exposed to low light, most of its energy is used in the photochemical photolysis of water and the subsequent reduction of CO_2 to high energy photosynthate. Under high light, the xanthophyll cycle pigments undergo epoxidation and now divert light energy to harmless heat rather than damaging excess light (Adams et al., 1999; Demmig-Adams, 1998). Again, the relatively slow activation of the cycle, or its 'switching' to the high light state, prevents, or at least minimizes, its beneficial, albeit costly, activity under fluctuating light.

f. RuBisCO - A dynamic model for photosynthesis was developed to elucidate the effect of flashing light that enhances the efficiency of photosynthesis. One particular feature of the model is that discrete RuBP particles circulate in the Calvin cycle and their speeds in the cycle are determined by the amount of ATP generated in the photon reception process. This can realize the light saturation under continuous light and the flashing light effect under fluctuating illumination. Laboratory experiments were conducted on *Chaetoceros calcitrans* (Yoshimoto et al., 2005).

All of the above lead us to the following conclusions:

a. Short duration periods of intense light are too brief to result in damage to the photosynthetic apparatus leading to photoinhibition of photosynthetic rates.

b. Short light periods do not allow sufficient time for the full activation of the xanthophyll-driven thermal energy dissipation of absorbed light, which would reduce the energy allocated to photochemistry.

c. Short light periods reduce the biomass losses incurred due to enhanced post-illumination respiration.

d. Dark intervals allow the regeneration and reoxidation of intermediate electron and CO_2 acceptors in the quinone pool and the Calvin cycle.

In summary, we can conclude that present developments allow better understanding of the mechanisms involved in the long-known enhancement of photosynthesis under fluctuating and flashing light. Future research will focus on defining the boundaries of the process in terms of irradiance levels, frequencies, and duty cycle. Regarding the mechanisms, these are likely to be explored in detail in order to understand their relative contribution under different conditions, and with more careful examination of the taxonomic differences in both characteristics and mechanisms.

2. Acknowledgments

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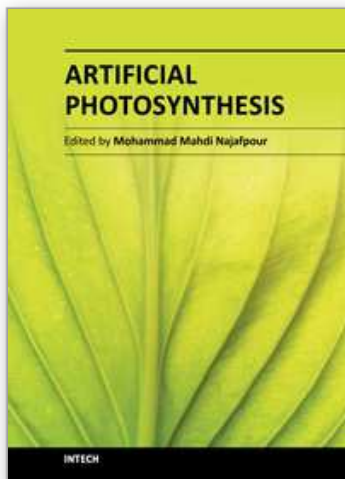
Photosynthesis is one of the most important reactions on Earth, and it is a scientific field that is intrinsically interdisciplinary, with many research groups examining it. We could learn many strategies from photosynthesis and can apply these strategies in artificial photosynthesis. Artificial photosynthesis is a research field that attempts to replicate the natural process of photosynthesis. The goal of artificial photosynthesis is to use the energy of the sun to make different useful material or high-energy chemicals for energy production. This book is aimed at providing fundamental and applied aspects of artificial photosynthesis. In each section, important topics in the subject are discussed and reviewed by experts.

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