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Influence of high frequency light/dark fluctuations on photosynthetic characteristics of microalgae photoacclimated to different light intensities and implications for mass algal cultivation

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Abstract

Oxygen evolution from a *Scenedesmus obliquus* dominated outdoor culture was followed in a small volume chamber, irradiated either by continuous white light or under light/dark frequencies between 0.05 to 5000 Hz, using arrays of 'high intensity' red light emitting diodes (LED's). By placing neutral density filters in the path of the white light, light saturation curves of the oxygen evolution (P/I curves) were measured using diluted aliquots of algal cultures. The results clearly showed that photosynthetic rates increased exponentially with increasing light/dark frequencies, that a longer dark period in relation to the light period does not necessarily lead to higher photosynthetic rates (efficiencies), and that algae do not acclimate to a specific light/dark frequency. One of the most important factors that influenced photosynthetic rates, either under continuous illumination or intermittent, was whether the algae were dark or light acclimated. Low light/dark frequencies were perceived by the algae as low light conditions, whilst the opposite was true for high frequencies. The light utilisation efficiency in a fluctuating light/dark environment depended on the acclimated state of the algae, the specific frequency of the fluctuations and the duration of the exposure. Since the frequencies determined the 'perceived' quantities of light, dark reactions played an important role in determining the average photosynthetic efficiencies. These results have important implications for algal biotechnology.

Introduction

The enhancement of photosynthesis by 'flashing light' (both the rate and the efficiency) has been known for many years (Kok, 1953). In mass algal cultures Richmond & Vonshak (1978) reported increased growth rates of *Spirulina* when the stirring speed was doubled. They ascribed the increase to a more favourable dark/light cycle due to increased turbulence. Laws et al. (1983) introduced wing-shaped foils into the flow path of their stirred mass cultures, which created vortex circulation's of about 0.5–1 Hz. This resulted in an almost doubling of productivity.

Terry (1986) found that the optimum enhancement of photosynthetic efficiencies occurred at frequencies ≥ 1 Hz, when the light intensity was high and the ratio of light/dark <1. Light/dark ratios of <1 would occur in mass algal cultivation systems when the optical density (biomass concentration) is such that all the light impinging on the surface is attenuated, before the light can reach the bottom in case of flat bed, or the middle in the case of tubular reactors. The ratio will become smaller as the areal density increases at any given light pathlength. Although conflicting results have been reported for algae when they are subjected to light/dark fluctuations in the medium (1 to 0.01 Hz) frequency range (Grobbelaar, 1989; 1991), Grobbe-

laar (1994) showed that a distinction should be made between the effects of light on the one hand and mixing on the other since these independently but also synergistically allows algae to utilise light more efficiently.

For convenience a distinction is made between three groups of light path lengths, i.e.;

- short light path (SLP) systems such as the thin-layered sloping ponds (TLS), flat plate bioreactors (PBR), immobilised cell systems and narrow diameter tubular reactors where the culture depth is less than 40 mm and mostly between 10–25 mm,
- medium light path (MLP) systems such as open raceways and large diameter tubular reactors where the culture is between 40–300 mm deep, but typically between 100–150 mm, and
- long light path (LLP) situations such as extensive production ponds (maturation ponds and some aquaculture systems) where the depth exceeds 300 mm. Natural systems will also be included in this category.

Outdoor open endless raceway ponds for the production of microalgal biomass belong to the MLP category and are mostly mixed with paddle wheels causing flow rates of 10 to 30 cm s^{-1}. Mixing in these systems are such that the frequency of the light/dark cycles are in the medium range (seconds to minutes). Grobbelaar (1989, 1991) showed that no enhancement of photosynthesis occurred at these frequencies when the rate of mixing is kept constant. These systems differ markedly from the TLS systems (Setlik et al., 1970), where at an average flow rates of 30 cm s^{-1}, much higher turbulencies are found. According to Doucha & Livansky (1995) the flow is turbulent with Reynolds Numbers of 3000 to 3200, which results in 'flashing light' light/dark frequencies. High flow rates and turbulencies would also be found in SLP tubular reactors (e.g. Bocchi et al., 1988). A further distinct difference between SLP and MLP systems is the much higher attainable biomass concentrations per volume culture in the former.

Legendre et al. (1986) stated that microalgae can adapt to the dominant frequencies of their environment. They found higher photosynthetic efficiencies when algae were subjected to fluctuating light, as compared to constant light, when the algae were taken from an environment of fluctuating light. These measurements were done on marine algae taken from an environment of high frequency light fluctuations.

In the TLS it is common practice to grow the algae to areal densities as high as 150 g (dw) m^{-2} and the rate of increase in biomass, from inoculation to harvesting is linear (Doucha & Livansky, 1995). Since this is very different from MLP systems and the most obvious difference is the light climate, we decided to investigate the influence of high frequency light/dark fluctuations (such as found in SLP reactors) on photosynthetic characteristics of microalgae, whether they photoacclimated to different light intensities and the implications for mass algal cultivation.

Material and methods

During the experimental period the microalgal population of the TLS ponds consisted mainly of *Scenedesmus obliquus* (TURP.) Kütz. strain 206 (Bartos, Cuba) and a *Chlorella* spp. The ratio in cell numbers between these two genera was about 2.3 and varied little. The design, preparation of the mineral culture media, supply of CO_2, inoculation and harvesting of the TLS are described in detail by Doucha & Livansky (1995).

Algae from the TLS ponds were used in the experiments either directly or after subcultivation in the laboratory. The main purpose of the laboratory cultures was to acclimate the algae to either high or low light. For the low light acclimation the algae were cultured in 50 ml tubes, suspended in a clear glass waterbath and illuminated from one side with a 150 W incandescent lamp. This gave a photon flux density of about 100 μmol photons m^{-2} s^{-1} at the surface of the tubes. The culture was continuously aerated with a 2% CO_2-enriched air mixture and the waterbath was maintained at 30 °C. High light acclimation was done under the same conditions as above, but illumination was from two 400 W Quartz Mercury Vapour lamps and the cell suspension was diluted regularly in order to limit self-shading. This gave a photon flux density of about 1500 μmol photons m^{-2} s^{-1} at the surface of the tubes.

Photosynthetic rates were measured as oxygen evolution at a steady state, using a small volume gas exchange chamber, described in detail by Bartos et al. (1975). Algal samples were diluted using fresh nutrient medium (no difference in the photosynthetic response was found between fresh nutrient medium and filtered culture solution) to a Chl *a* concentration of about 6 mg L^{-1} prior to the oxygen measurements (Grobbelaar et al., 1995). Calibration and measurement of the photosynthesis/irradiance response (P/I) was done essentially as described by Dubinsky et al. (1987). All the measurements were done at 30 °C. The photosynthetic response to light/dark fluctuations was also measured in the small volume gas exchange chamber. The exper-

imental set-up was arranged such that the chamber was illuminated from both sides with arrays of forty high bright red LED's (light emitting diodes at 660 nm) each array mounted on a discs. The maximum intensity at continuous illumination was about 800 μmol photons m^{-2} s^{-1} inside the chamber. The LED's were switched 'on' and 'off' using a digital pulse generator in conjunction with a high capacity regulated power supply. The cycles were either of equal duration indicated by 1L/1D or where the dark period was double that of the light period it was indicated by 1L/2D. The results are mostly shown for the time interval of one unit of light. For example when the time unit was 1 ms the frequency at 1L/1D was 500 Hz and at 1L/2D it was a pulsed frequency of 333.3. The recorded slopes of O_2 concentration were used to determine the photosynthetic rates and these were normalised with the Chl *a* content to give μmol O_2 mg Chl a^{-1} h^{-1}. From the P/I curves α^B, the maximum chlorophyll specific photosynthetic efficiency as μmol O_2 mg Chl a^{-1} h^{-1} [μmol photons m^{-2} s^{-1}]$^{-1}$, P^B_{max}, the maximum chlorophyll specific production rate as μmol O_2 mg Chl a^{-1} h^{-1} and I_k, the light intensity at the onset of light saturated photosynthesis in μmol photons m^{-2} s^{-1} were determined (see also Grobbelaar et al., 1995).

Chlorophyll *a* and the carotene/xanthophyll mixture (hereafter referred to only as carotene) were extracted in 95% acetone and measured spectrophotometrically (Shimadzu dual wavelength/dual beam UV-3000 spectrophotometer). The equations of McKinney (1941) with the modifications by Arnon (1949) were used to calculate the pigment concentrations.

The algae were acclimated to light/dark frequencies of equal duration of 0.05, 0.5, 5, and 50 Hz, for periods up to 72 hours in a 20 ml container surrounded by an array of one hundred LED's. CO_2 enriched air was supplied to the culture, which was diluted daily with fresh nutrient medium to an approximate Chl *a* concentration of 5 mg L^{-1}. Bubbling with CO_2 enriched air ensured that the culture was thoroughly mixed.

Results

P/I curves of samples taken from two TLS ponds at different cell densities are shown in Figure 1. The less dense culture (A) had a P^B_{max} of 714 μmol O_2 mg Chl a^{-1} h^{-1} while it was 482 μmol O_2 mg Chl a^{-1} h^{-1} for the more dense culture. I_k, for the less dense culture was 440 μmol photons m^{-2} s^{-1}, while for the more dense culture it was 302 μmol photons m^{-2} s^{-1}.

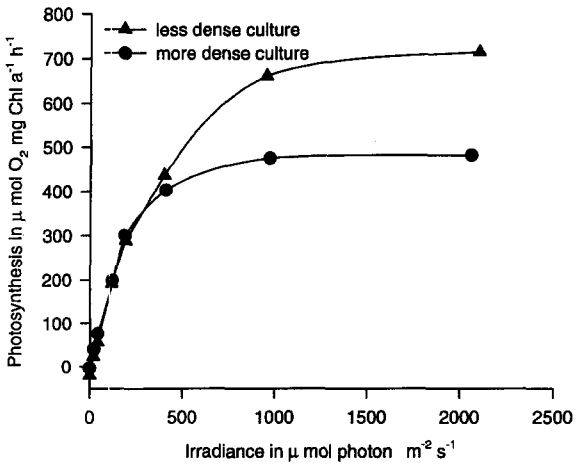

Figure 1. P/I curves of algae collected from outdoor TLS ponds, where the less dense culture had a biomass concentration of 3.0 g (dw) L^{-1} and the more dense culture a biomass concentration of 5.7 g (dw) L^{-1}.

The intensity of the LED flashes was well above the Ik intensities and clearly in the saturating photon flux densities. There were little difference in α^B between the two cultures. The less dense culture exhibited characteristics of high light (HL) acclimated cells and the more dense culture that of low light (LL) acclimated cells, which is in agreement with the findings of Grobbelaar et al. (1995). Subjecting the algae from these two cultures to light/dark frequencies where the time unit of the light period ranged from 10 s to 0.1 ms, either at cycles of equal duration or when the dark period was double that of the light period, showed that the photosynthetic rates increased exponentially with an increase in the frequencies (Figure 2). The overall rates were higher for the algae from the more dense culture (Figure 2B) when compared to the algae from the less dense culture (Figure 2A). The algae that were subjected to 1L/2D received a third less light than the ones that received 1L/1D per unit time. The average photosynthetic rate of the 1L/2D treatments, over the range of light/dark frequencies for the less dense culture, was 0.65 that of the 1L/1D (Figure 2A) and for the more dense culture it was 0.59 (Figure 2B). The data also shows a fairly constant difference between the 1L/1D and the 1L/2D treatments over the examined frequency range.

Had the algae adapted to any specific frequency in the outdoor ponds, one would have expected a peak rate, over the range of frequencies tested. The results shown in Figure 2 clearly show that this was not the

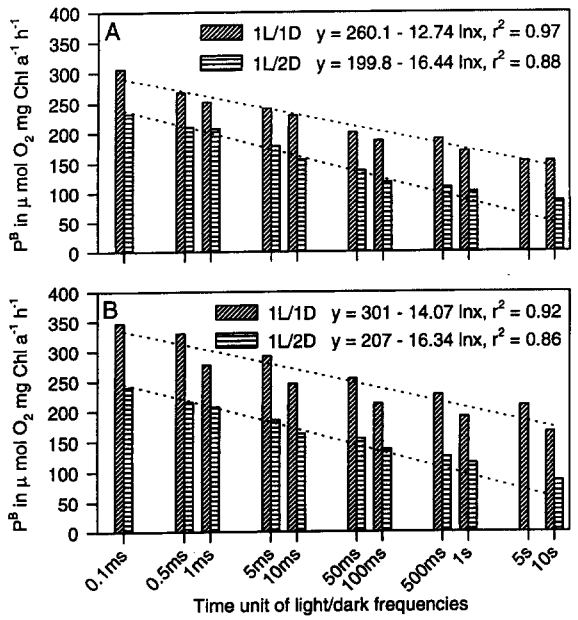

Figure 2. Photosynthetic rates of algae taken from the outdoor ponds and subjected to increasing frequencies of light/dark cycles. A = algae from the less dense culture (see Figure 1) and B = algae from the more dense culture. 1L/1D = equal duration of light and dark periods and 1L/2D = a dark period double that of the light period.

Table 1. The ratio of average photosynthetic rates at increasing fluctuating frequencies between the 1L/2D and 1L/1D acclimated algae (data from Figures 3 to 5) (acclimation time of the 50 Hz culture were 20, 44 and 68 h)

Acclimated frequency inHz	Acclimation time 24 h	48 h	72 h
0.05	0.77	0.78	0.68
0.5	0.66	0.65	0.78
5	0.69	0.83	0.70
50	0.67	0.84	0.71

case. In order to test whether the algae can acclimate to a specific frequency, they were grown in the laboratory at 1L/1D frequencies of 0.05, 0.5, 5 and 50 Hz for 72 hours. The results for the 0.05, 0.5 and 50 Hz frequencies are shown in Figures 3, 4 and 5, respectively. From these results it is clear that the photosynthetic rates always increased exponentially with increasing frequency. However, the following major trends were seen, i.e.:

- The differences between the 1L/2D and 1L/1D ratio's were generally higher than 0.66, the highest being 0.84 over the frequency range (Table 1). Hence the long-term integral of light energy utilisation indicated that light energy is generally used more efficiently at the 1L/2D ratio's (0.66 being the difference in light exposure between the 1L/2D and 1L/1D treatments), compared to the 1L/1D ratio's.
- In three of the four experiments an acclimation to the L/D frequencies were seen, where the highest ratio's were measured after 44 or 48 h of exposure (Figures 3B and 5B). However, no frequency specific acclimation could be seen.
- The higher the light/dark frequencies the smaller were the differences between the photosynthetic rates of the 1L/2D and the 1L/1D treatments (Figures 3B, 4C, 5B and 5C).
- The highest overall photosynthetic rates were measured in the culture exposed to 0.05 Hz light/dark cycles (Figure 3).

Grobbelaar et al. (1995) concluded that algae acclimate to the overall light climate in outdoor cultures, where they change from high light acclimated after inoculation to low light acclimated cells before harvesting and in view of the differences between the algae taken from the outdoor ponds (Figures 1 and 2), we decided to investigate the influence of light modulations on algae which were either high or low light acclimated. Samples from the outdoor ponds were cultured in the laboratory at either 100 or 1500 μmol photons m^{-2} s^{-1} for 48 h. Their photosynthetic response to increasing frequencies of light/dark fluctuations are shown in Figures 6 and 7. The algae grown at low light (low light acclimation) showed an increase in photosynthetic rates at higher frequencies and the 1L/1D ratio always gave higher rates than the 1L/2D ratio (Figure 6). However, the difference between the 1L/1D and the 1L/2D became smaller, the longer the algae were kept under low light conditions. After 6 h the ratio of (1L/2D)/(1L/1D) was on an average 0.65, after 24 h it was 0.70 and after 48 h it was 0.79. This indicated that the algae became progressively more efficient in the overall utilisation of light energy when the dark period was longer than the light period. Such conditions would typically be found in highly dense cultures (e.g. prior to harvesting).

Following 6 h of acclimation to high light the algae (Figure 7) showed an initial increase in the photosynthetic rates with increasing light/dark frequencies and the average rate of the 1L/2D was 57% that of the 1L/1D. The overall rates decreased after 20 h exposure and the difference between the 1L/1D and the 1L/2D was only 19% (results not shown). After 24 h exposure (Figure 7B), low photosynthetic rates were measured

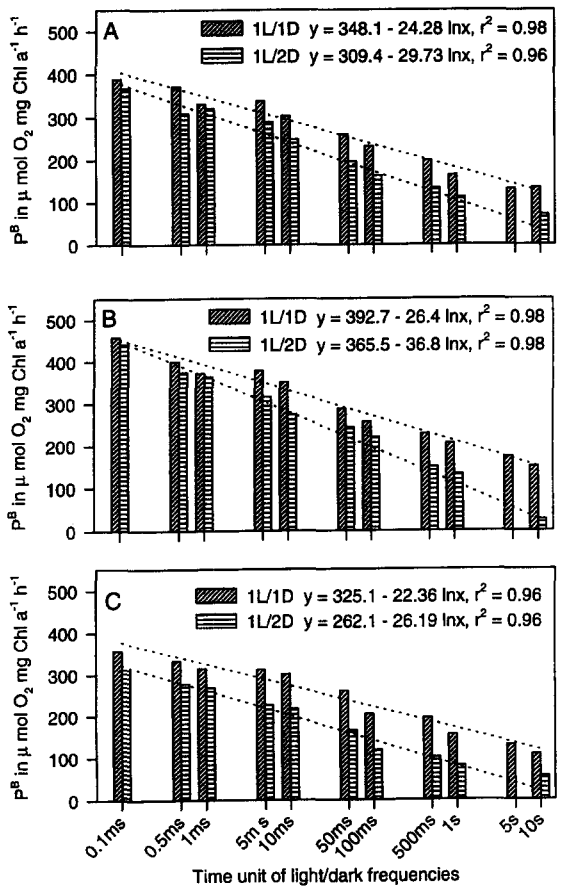

Figure 3. Photosynthetic rates of algae grown at light/dark cycles of 10 s light/10 s dark (0.05 Hz) and then subjected to increasing light/dark frequencies. A = algae grown for 24 h, B = 48 h and C = 72 h. 1L/1D = equal duration of light and dark periods and 1L/2D = a dark period double that of the light period.

at the low frequencies (0.05 to 1 Hz) and the 1L/2D yielded on an average 23% higher photosynthetic rates than the 1L/1D. Per unit light energy integrated over time, these algae were more than 50% more efficient than the algae that were exposed to 1L/1D frequencies. These algae, therefore, 'preferred' longer dark periods to light periods in an oscillating light field. After 48 h exposure the opposite is seen and 1L/1D gave higher photosynthetic rates than the 1L/2D. Also apparent is that the rates of the 1L/2D remained essentially constant until a frequency of 100 Hz, whereafter it increased with increasing frequency. An important aspect when interpreting the above data, is that the Chl *a*/Car ratio decreased by more than 60% during the 48 h period, where the Chl *a* content decreased only slightly, but the carotene content more than doubled.

We noticed that the high light acclimated algae generally had much lower overall photosynthetic rates, compared to the low light acclimated algae, when the dark period in relation to the light period was increased. In order to quantify this the compensation (point where the oxygen concentration = 0 and does not change with time in the photosynthetic chamber) light/dark ratio's at frequencies of 0.5 to 5000 Hz for both the low light and the high light acclimated algae were measured. The high light acclimated algae always had higher compensation light/dark ratios than the low light acclimated ones and the ratios decreased with an increase in the frequencies (Figure 8). The results also show that the longer the acclimation the higher was the compensation light/dark ratio (Figure 8B), indicating that the algae become more efficient in utilising small quantities of light energy over periods of time.

Discussion

The following three conclusions are immediately apparent from the results:

- Photosynthetic rates increased exponentially with increasing light/dark frequencies,
- A longer dark period relative to the light period does not necessary lead to higher photosynthetic rates (efficiencies), and
- Acclimation to a specific frequency, in the range and with the resolution tested did not take place.

Our data supports the findings of e.g. Kok (1953) and others, that light/dark cycles >1 Hz causes an increase in photosynthetic rates and light utilisation efficiencies. This increase was exponential, but varied markedly between the different treatments. Quantitatively this is clearly indicated from the slopes of the regressions, where they ranged from 11.5 to 36.8 μmol O_2 mg Chl a^{-1} h^{-1} [time duration if L/D cycle]$^{-1}$ (Figures 2 to 7). In general we found large variations in the photosynthetic rates, both in the response to increased light/dark frequencies a, well as to the ratio of light/dark periods.

In general our results support the conclusions of Terry et al. (1986). However, it is important also to consider photosynthetic differences at specific light/dark frequencies and the light acclimation state of an alga. In our experiments the 1L/2D received 0.66 the light flux per unit time, compared to the light quantity of the 1L/1D. Under certain conditions we either found

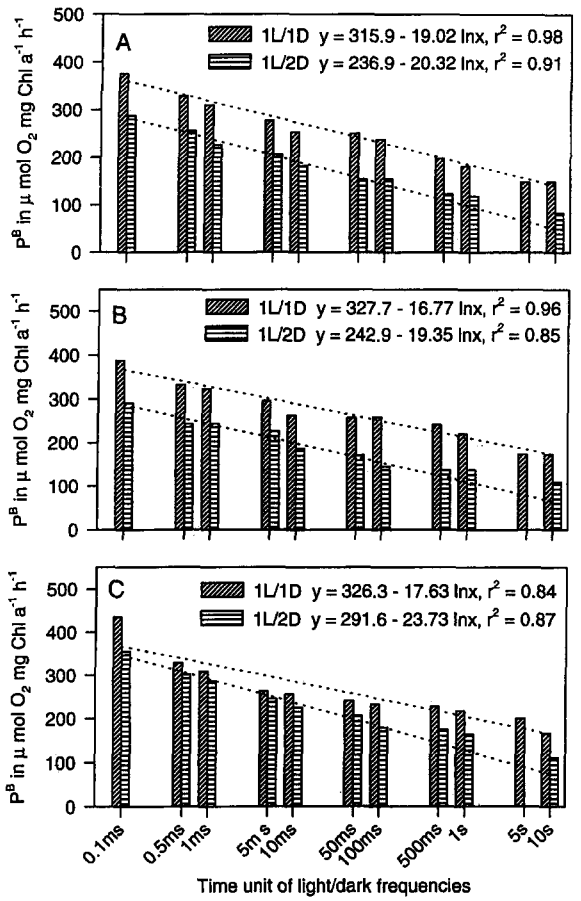

Figure 4. Photosynthetic rates of algae grown at light/dark cycles of 1 s light/1 s dark (0.5 Hz) and hen subjected to increasing light/dark frequencies. A = algae grown for 24 h, B = 48 h and C = 72 h. 1L/1D = equal duration of light and dark periods and 1L/2D = a dark period double that of the light period.

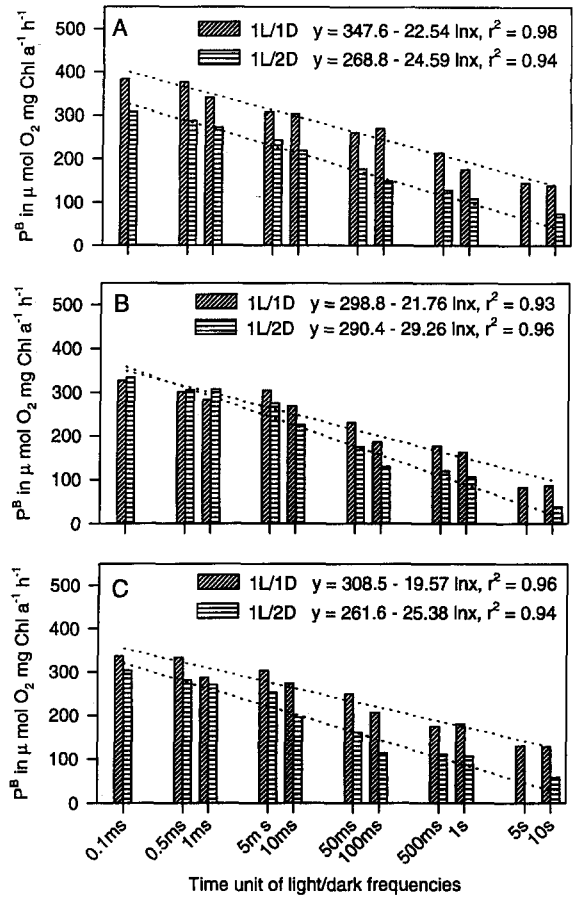

Figure 5. Photosynthetic rates of algae grown at light/dark cycles of 10 ms light/10 ms dark (50 Hz) and then subjected to increasing light/dark frequencies. A = algae grown for 20 h, B = 44 h and C = 68 h. 1L/1D = equal duration of light and dark periods and 1L/2D = a dark period double that of the light period.

an enhancement, no enhancement and even inhibition (Figures 2–7). For example the average photosynthetic rate at 1L/2D, after high light exposure for 48 h (Figure 7C) was 0.56 times that of the 1L/1D cycles, whilst it was 1.23 times after an exposure of 24 h (Figure 7B).

In our experimental set-up, we could not show that the algae acclimated to a particular frequency as reported by Legendre et al. (1986), even after exposing them for 72 h to a specific frequency. Whether this was still to short needs to be tested and it should be remarked that in nature time scales of this length, without interruption, would for all practical purposes not exist. However, as stated above, our results showed a variable response to different light/dark modulations, by either increasing or decreasing their integral photosynthetic efficiencies depending on the specific conditions to which they were subjected and their light history. The largest variation from the generally observed exponential increase in photosynthetic rates with increased light/dark frequencies were seen for the high light exposed alga (Figure 7).

In continuous light, high light acclimated algae had the highest maximal photosynthetic rates (Figure 1). However, the converse was seen in modulated light, where low light acclimated algae had higher photosynthetic rates (Figures 2 to 7). We are of the opinion that one of the most important factors that influences photosynthetic rates, either in continuous or intermittent illumination, is whether the algae show characteristics of light or dark acclimation (see Falkowski et al., 1994; Grobbelaar et al., 1995). The results shown in Figure 7 clearly indicate that major changes took place in the

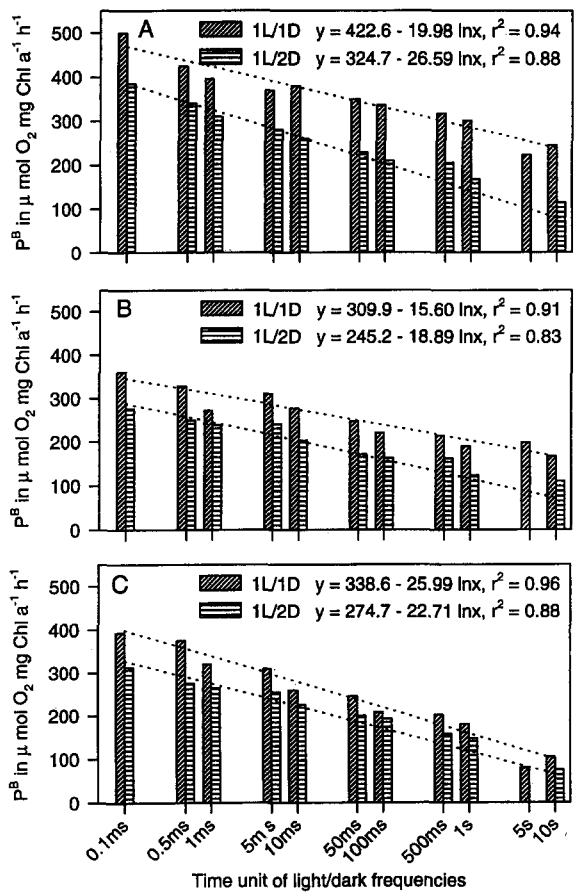

Figure 6. Photosynthetic rates of low light exposed algae grown at 100 μmol photon m^{-2} s^{-1} and subjected to increasing light/dark frequencies. A = algae acclimated for 6 h, B = 24 h and C = 48 h.

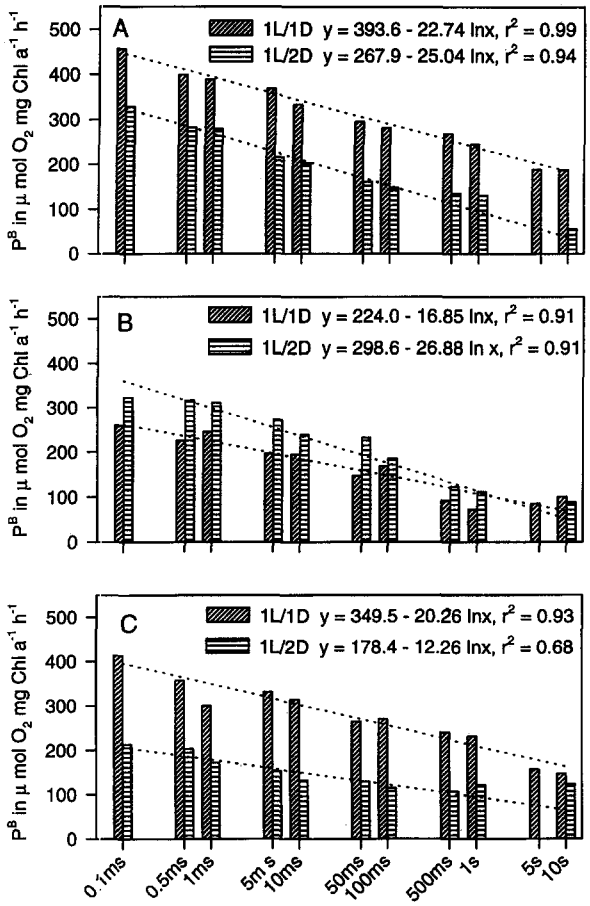

Figure 7. Photosynthetic rates of high light exposed algae grown at 1500 μmol photon m^{-2} s^{-1} and subjected to increasing light/dark frequencies. A = algae acclimated for 6 h, B = 24 h and C = 48 h.

response of the algae to different frequencies and ratios of light/dark cycles, where the algae acclimated to high light conditions during the course of this experiment. High light/dark frequencies of high intensity, effectively causes photosynthetic rates to increase which is analogous to an increase in the intensity of continuous irradiance and this leads to high light acclimated characteristics (see also Figure 5). At low light/dark frequencies, high light acclimated algae perceive low light conditions and the light energy over a period of time, is utilised inefficiently (Figures 7). Important in interpreting the results shown in Figure 7 is the increase in the carotene content of the cells. After 24 h of exposure the photosynthetic rates were depressed and the algae were stressed. After 48 h they had acclimated by producing large quantities of the photoprotective carotene pigments and essentially recovered their initial photosynthetic capacity. On the other hand the low light acclimated algae were able to progressively utilise less light energy better, as shown in Figure 6. After 6 h of exposure the 1L/2D cells produced 65% that of the 1L/1D, after 24 h it was 70% and after 48 h it was 79%. This is an increase in photosynthetic integral light utilisation efficiency of almost 22% over the 48 h period. Long light/dark oscillations also had the effect that the algae became low light acclimated, as shown in Figure 3 with high overall photosynthetic rates and the ratio of (1L/2D)/(1L/1D) being well above 0.66.

High versus low light acclimation also influences the compensating photosynthetic energy requirements response (Figure 8). The light intensity at which neither an increase nor a decrease in the oxygen concentration took place, clearly showed that low light acclimated algae needed much less light energy per unit time than

high light acclimated ones. This difference became progressively larger as the duration of the light pulse decreased, where e.g.: 1 ms of light in a 60 ms interval was sufficient to maintain the compensation point at the ms time scale (Figure 8A), compared to 1 s of light in an interval of 8 s at the s time scale. From the results it is clear that four factors played a role in determining the compensation light/dark ratio, i.e.:

- the duration of the light flash,
- the light acclimation state of the algae,
- the immediate light history, and
- the intrinsic respiratory (maintenance) characteristics of an algae.

Other than the direct increase in photosynthetic efficiencies in modulating light fields of high frequency, dark reactions (respiratory rates) determine most of the observed variations in the photosynthetic rates. In continuous light, high maximum photosynthetic rates were seen for high light acclimated algae and vice versa (Figure 1). Under high light conditions, high respiration rates ensures high metabolic rates and the sufficient enzymes present ensure high production rates (carbon-fixing and oxygen liberation). This advantage is lost in a modulated light field, due to differences in the overall dark reaction and dark induction rates, where the high light acclimated algae require longer dark periods to metabolise the fixed carbon. Because of this the overall rates of the high light acclimated algae had lower photosynthetic rates at equivalent light/dark oscillations than the low light acclimated algae (Figures 2 to 7). Also when the dark period was increased as with the 1L/2D treatments the higher rates in comparison to the 0.66 difference in the quantity of light energy of the 1L/1L treatments, clearly indicated the importance of a dark period for the metabolism of the trapped photosynthetic energy. It is well known that dark respiration rates depend on the light history of an alga, where it is high following exposure to high illumination, becoming progressively less as the intensity of the pre-illumination decreases as well as the time in the dark (Falkowski & Owen, 1978; Grobbelaar & Soeder, 1985). Our results, furthermore, (Figure 8) clearly showed that high light acclimated cells have high dark respiration rates and therefore, needed either relatively high light intensities to reach compensating photosynthetic rates or high frequently light dark cycles. The converse was seen for low light acclimated algae.

The results presented have important practical implications for algal biotechnology. During the growth cycle in a batch process there is a progressive transition from high light conditions (after inoculation) to low light conditions (prior to harvesting) and the algae displays high light acclimated followed by low light acclimated characteristics (Grobbelaar et al., 1995 and Figure 1). During this transition the light conditions in the profile changes, both in quantity and quality because the algal mass selectively absorbs different wave-lengths. Under mixed or turbulent conditions the cells are progressively subjected to light/dark modulations, from initial slight modulations to light/dark cycles of even duration when the light is completely attenuated over the culture depth, to conditions where the dark period is longer than the light period, i.e. when the biomass concentration is so high that the photic zone is less than the aphotic zone. The rate of mixing and the thickness of the culture suspension furthermore, determines the frequencies of the light/dark modulations. In MLP systems light/dark fluctuations are in the range of seconds to minutes. Photosynthetic rates are low under such conditions (see the 5 and 10 s frequency rates shown in Figures 2 to 7) indicating that over time light energy is used inefficiently. Under

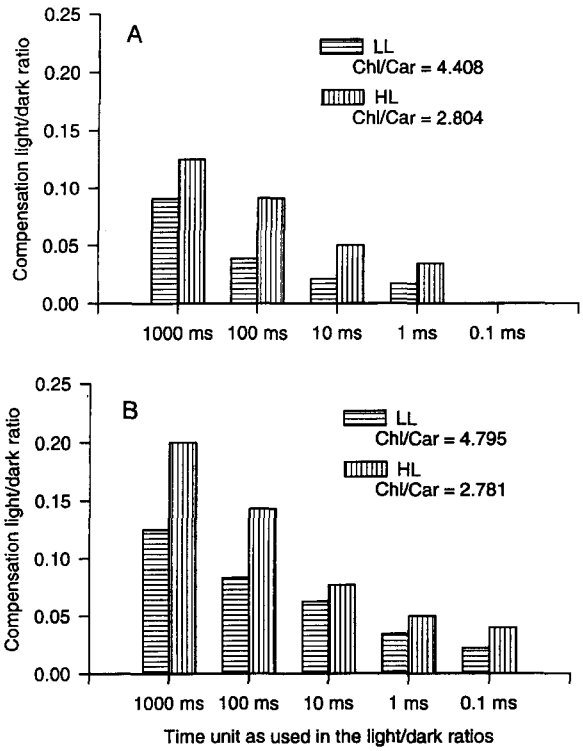

Figure 8. Compensation light/dark ratios, where the oxygen evolution = 0, against different light/dark frequencies for low light (LL) and high light (HL) acclimated algae. The results shown in A were after an exposure of 5 h and that of B after 48 h.

these conditions the compensation light/dark ratio is relatively high (see e.g. 1000 ms interval shown in Figure 8). Consequently productivities would be low and the attainable biomass densities would also be low. Another factor limiting production rates in MLP systems is the losses of light energy due to the absorption thereof by the large aqueous portion in relation to autotrophic biomass. In SLP culture systems where the mixing rates are high, short light/dark frequencies manifest resulting in high photosynthetic rates (see e.g. the 1 ms and shorter frequencies shown in Figures 2 to 7) and the compensation light/dark ratio is small (see e.g. the 1 ms interval in Figure 8). Under such conditions high average light utilisation efficiencies, high photosynthetic rates and high biomass concentrations would be favoured. High biomass concentrations would also means less light losses due to a smaller aqueous fraction in relation to the autotrophic fraction. This clearly has practical implications, where SLP algal production reactors have definite advantages over MLP and even LLP systems, not only in terms of higher attainable biomass concentrations, but also higher average light utilisation efficiencies, lower compensation light/dark ratios and consequently higher production rates.

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