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Mechanisms of Photoacclimation on Photosynthesis Level in Cyanobacteria

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1. Introduction

Cyanobacteria are oxygenic photoautotrophic prokaryotes, which develop in many aquatic environments, both freshwater and marine. They successfully grow in response to increasing eutrophication of water, but also because of shifts in the equilibrium of ecosystems (Stal et al., 2003). Cyanobacteria possess many unique adaptations allowing optimal growth and persistence, and the ability to out-compete algae during favorable conditions. For instance, many species are buoyant due to the possession of gas vesicles, some of them are capable of fixing N_2 , and unlike algae, which require carbon dioxide gas for photosynthesis, most cyanobacteria can utilize other sources of carbon, like bicarbonate, which are more plentiful in alkaline or high pH environments. The cyanobacteria live in a dynamic environment and are exposed to diurnal fluctuations of light. Planktonic species experience differences in irradiance when mixed in the water column (Staal et al., 2002), whereas mat-forming cyanobacteria are exposed to changes in light intensity caused by sediment covering or sediment dispersion. Such rapidly changing environmental factors forced photoautotrophic organisms to develop many acclimation mechanisms to minimize stress due to low and high light intensities. High irradiance may damage photosynthetic apparatus by photooxidation of chlorophyll *a* molecules. Some carotenoid pigments may provide effective protection against such disadvantageous influence of light (Hirschberg & Chamovitz, 1994; Steiger et al., 1999; Lakatos et al., 2001; MacIntyre et al., 2002). Photosynthetic organisms respond to decreased light intensity by increasing the size or/and the number of photosynthetic units (PSU) whose changes, in turn, can be reflected in characteristic patterns of P-E curves (Platt et al., 1980; Prézelin, 1981; Ramus, 1981; Richardson et al., 1983; Henley, 1993; Dring, 1998; Mouget et al., 1999; MacIntyre et al., 2002; Jodłowska & Latała, 2010). Variation in α and P_m (expressed per biomass or per chlorophyll *a* unit) plays a key part in interpreting physiological responses to changes in environmental conditions.

The aim of this review was to present exceptional properties of two different cyanobacteria, planktonic and benthic, their abilities to changing environmental condition, especially to irradiance. This information would be helpful in understanding the phenomenon of mass formation of cyanobacterial blooms worldwide, and would be very useful to interpret the domination of cyanobacteria in water ecosystem in summer months.

2. Light as a major factor controlling distribution, growth and functionality of photoautotrophic organisms

Light is one of the main trophic and morphogenetic factors in the life of photosynthetic organisms. Intensity, quality and the time of light impact affect photosynthesis, which is responsible for producing organic matter, cell division and the growth rate of organism. The positive effect of increasing light intensity states only to a point, after which stabilization or even a drop in cell division takes place (Ostroff et al., 1980; Latała & Misiewicz, 2000).

Effect of light on organisms can be investigated in two ways, firstly in ecological perspective i.e. paying special attention to the influence of this factor on distribution, and secondly in physiological point of view studying mechanisms of acclimation facilitating to survive in changing environmental conditions. Light is one of the main factors controlling the distribution of photoautotrophs in water column demonstrating their light preferences. Similarly to vascular plants, algae and cyanobacteria may also indicate their shadow-tolerant features or heliophylous character (Falkowski & La Roche, 1991). This phenomenon is observed both in case of benthic forms attached to the bottom and planktonic form floated in water column. Shadow-tolerant autotrophs concentrate in deeper water, where intensity of light is significantly lower, whereas heliophylous ones, preferring higher light intensity to growth and functionality, live in shallows. However, at surface layer of water phototrophic organisms are exposed to harmful effect of very high intensity of light and also effect of ultraviolet radiation, what may cause photoinhibition. Moreover, at deep water body we can define the level, below which photoautotrophic life gradually disappeared. The depth, at which anabolic and catabolic processes are balanced, is named as compensation level. Below this level light condition are insufficient, so that photosynthetic organisms are not able to normally develop and reproduce (Falkowski & La Roche, 1991).

In natural conditions, phytoplankton which is vertically transferred within the euphotic zone experience not only changes of intensity but as well spectral quality (Rivkin, 1989). Spectral composition of downwelling light change progressively with increasing depth. Changes in spectral quality depend on the absorption spectra and scattering of the suspended particles within the water column and on absorption of water itself and the angle at which light impinges the water surface (Staal et al., 2002). In regions poor in nutrients the longer wavelengths are selectively absorbed within the upper ca 10 m and only blue-green light remains. However, in coastal regions rich in biogenic substances and yellow substances the shorter wavelengths are rapidly absorbed (Kirk, 1983; Rivkin, 1989).

When autotrophic organisms experience changes in light regime, both intensity and spectral quality, acclimation of photosynthetic apparatus to variable light condition is observed. Photoacclimation of these organisms is linked to alterations in total cellular concentration of light-harvesting and reaction centre pigments, and also in the ratio of different pigments. Generally, one observes an inverse correlation between light intensity and pigment content: the less light energy available, the more photosynthetic pigments are synthesized by the cells (Tandeau de Marsac & Houmard, 1988). According to the idea proposed by Engelmann in 1883 different groups of marine algae dominate the benthic vegetation at different depths because their pigment composition adapts them for absorption, and hence photosynthesis, in light quality that prevails at that depth. This phenomenon is known as chromatic adaptation. It has often been pointed out that this concept is based on extremely superficial generalizations about the vertical distribution of benthic algae, since the representatives of most of the major groups can be observed at most depths (Dring, 1992). Laboratory studies

of marine algae grown at different light intensities and different light spectrum suggest that phenotypic variations in pigment composition with depth are controlled by the irradiance level and not by the quality of the light (Ramus, 1981; Dring, 1992). However, the effect of light wavelength on pigment content of the cells appears to be restricted to some cyanobacteria. Changes in cell pigmentation in response to spectral quality of light result from modifications of the relative amounts of phycoerythrin (PE) and phycocyanin (PC). These phycobiliproteins are the major light-harvesting pigments used to drive photosynthesis. Only cyanobacteria which are able to synthesize PE can undergo complementary chromatic adaptation (Tandeau de Marsac & Houmard, 1988). Light quality may be important factor controlling and regulating metabolic processes in algae and cyanobacteria, however in this study we consider to discuss the effect of changes of light intensity on photoacclimation on photosynthesis level.

3. Photosynthesis and light response curves

The photosynthesis rate achieved by a photoautotroph cell depends on the rate of capture of quantum of light. Certainly, this is determined by the light absorption properties of the photosynthetic biomass, composition of photosynthetic pigments in the cell and by the intensity and spectral quality of the field (Kirk, 1996).

The relationship between photosynthesis rate and light intensity is well described by photosynthetic light response curves (P-E). P-Es are very useful tools to predict primary productivity, and their analysis provides a lot of valuable information about photoacclimation mechanisms of cells (Platt et al., 1980; Ramus, 1981; Richardson, 1983; Henley, 1993; Dring, 1998; MacIntyre et al., 2002). The changes in concentration of chlorophyll *a* and other photosynthetic pigments in cell influence the course of P-E curves, which illustrate maximum rate of photosynthesis (P_m), the initial slope of photosynthetic curves (α), the compensation (P_c) and saturation irradiances (E_k ; the intercept between the initial slope of P-E and P_m) and dark respiration (R). The initial slope of photosynthetic curves at limiting light intensity (α) is a function of both light-harvesting efficiency and photosynthetic energy conversion efficiency (Henley, 1993). An increase of chlorophyll *a* concentration in the cell of photoautotrophic organism improves the effective absorption of light, what causes an increase of the P-E slope, in case the rate of photosynthesis is expressed in biomass unit. However, if photosynthesis is expressed in chlorophyll unit, it will not be observed the variability of α parameter. It is because of the photosynthetic rate at the limiting light intensity is proportional to the concentration of chlorophyll *a* (Dring, 1998). The chlorophyll *a* is arranged in the thylakoid membranes in photosynthetic units (PSU), each of which consists of 300-400 chlorophyll molecules associated with a single reaction centre. An increase in pigment concentration could be achieved either by building extra molecules into the existing PSUs without changing the number of reaction centers (called as a change of PSU size) or by building up complete new PSUs without changing their size (called as a change of PSU number) (Dring, 1998). These two mechanisms of photoacclimation have quite different effects on values of P_m . Since P_m is related to the number of reaction centers available, an increase in the size of PSUs have no effect on the maximum photosynthesis in biomass unit, that is why the photoautotrophs with different concentration of chlorophyll *a* have different P-E slope, but the same value of P_m . If, however, the photosynthesis rate is expressed in chlorophyll *a*, the value of P_m will drop with an increase of chlorophyll *a* concentration, but the P-E slope remains constant.

However, when the number of PSUs increases proportionally to the increase in chlorophyll *a* concentration, the maximum photosynthesis in biomass unit will also increase in proportion to the chlorophyll *a* concentration, but this means that P_m in chlorophyll unit will be constant (Dring, 1998). According to the Ramus (1981) model, if the number of PSUs increases, more quantum of light is necessary to saturate the photosynthesis (higher E_k and P_m), but if only the size of PSUs increases without any change of their number, not much light will be needed to saturate the photosynthesis (lower E_k and P_m). In the second case, PSU will be working more effectively (Lobban and Harrison, 1997).

4. Photoacclimation strategies in two strains of cyanobacteria: Planktonic *Nodularia spumigena* and benthic *Geitlerinema amphibium*

Cyanobacteria are very interesting material to study relationships between biological activity of organism and various environmental factors, because they often exist in extreme circumstances and can acclimate efficiently to changing environmental conditions (Latała & Misiewicz, 2000).

The experiments were conducted on two different strains of Baltic cyanobacteria: planktonic *Nodularia spumigena* and benthic *Geitlerinema amphibium*. The investigated strains were isolated from southern Baltic Sea, exactly from the coastal zone of the Gulf of Gdańsk, and now they were maintained as unialgal cultures in the Culture Collection of Baltic Algae (CCBA) (<http://ccba.ug.edu.pl>) at the Institute of Oceanography, University of Gdańsk, Poland (Latała et al., 2006). Buoyant cyanobacteria, like *N. spumigena*, previously mixed throughout the water column, float to the surface of water, where their cells are exposed to full sunlight, and this abrupt change in irradiance may induce photoinhibition (Ibelings, 1996). This species of cyanobacterium always occurs at water temperatures over 18°C and during weather conditions conducive to water column thermal stratification (Hobson et al., 1999). It is one of the filamentous cyanobacteria, which regularly occurs in the Baltic water in summer and often forms toxic blooms. *N. spumigena* grows especially well in the illuminated upper layer of the euphotic zone. In the Baltic Sea, it is most abundant to depths of 5 m (Hajdu et al., 2007), but it is also observed as deep as 18 m (Stal & Walsby 2000; Jodłowska & Latała, 2010). Similarly, mat-forming cyanobacterium, like *G. amphibium*, experience changes in light regime. These organisms may periodically be covered by a layer of sediment, which limits availability of light. On the other hands, sediment dispersion can lead to a rise in light intensity. *G. amphibium*, as a permanent element of summer microbial mats in the Gulf of Gdańsk (Southern Baltic) (Witkowski, 1986), may be an example of how organisms make use of their outstanding acclimation ability in the best possible way (Jodłowska & Latała, 2010).

According to literature data cyanobacteria are generally recognized to prefer low light intensity for growth and photosynthesis (Fogg & Thake, 1987; Ibelings, 1996). However, the investigated strain of *N. spumigena* was found to be well acclimated to relatively high light intensity (290 $\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), which was especially evident within the range of temperature 15-20°C (Fig. 1A). The factorial experiments with *N. spumigena* showed that irradiance had a promoting effect on cyanobacterial concentration, but the interaction between increasing irradiance of over about 100 $\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and increasing temperature over about 23°C inhibited the filament concentration. Prolonged exposure to high light intensity may cause photoinhibition, and induce harmful effects resulting from

increased temperatures. Optimal growth conditions were noted at about 180-290 $\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and 15-17°C. The maximum number of filament units (about $5\cdot 10^5$ filament units ml^{-1}) was about 10x greater than the minimum one. Similarly, the factorial experiments on *G. amphibium* showed that both irradiance and temperature have promoting effect on cyanobacterial culture concentration, but this positive effect was observed up to 120 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ at 35°C as well as up to 170 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ at 30°C (Fig. 1B). However, the interaction between temperature of 35°C and light intensity of 170 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ resulted in growth inhibition (Latała & Misiewicz, 2000). An excess of light energy absorbed by photosynthetic pigments together with high-temperature stress may accelerate photoinhibition by inhibiting the repair of photodamaged PSII (Allakhverdiev et al., 2008; Takahashi & Murata, 2008; Takahashi & Badger, 2011). Richardson & her co-workers (1983)

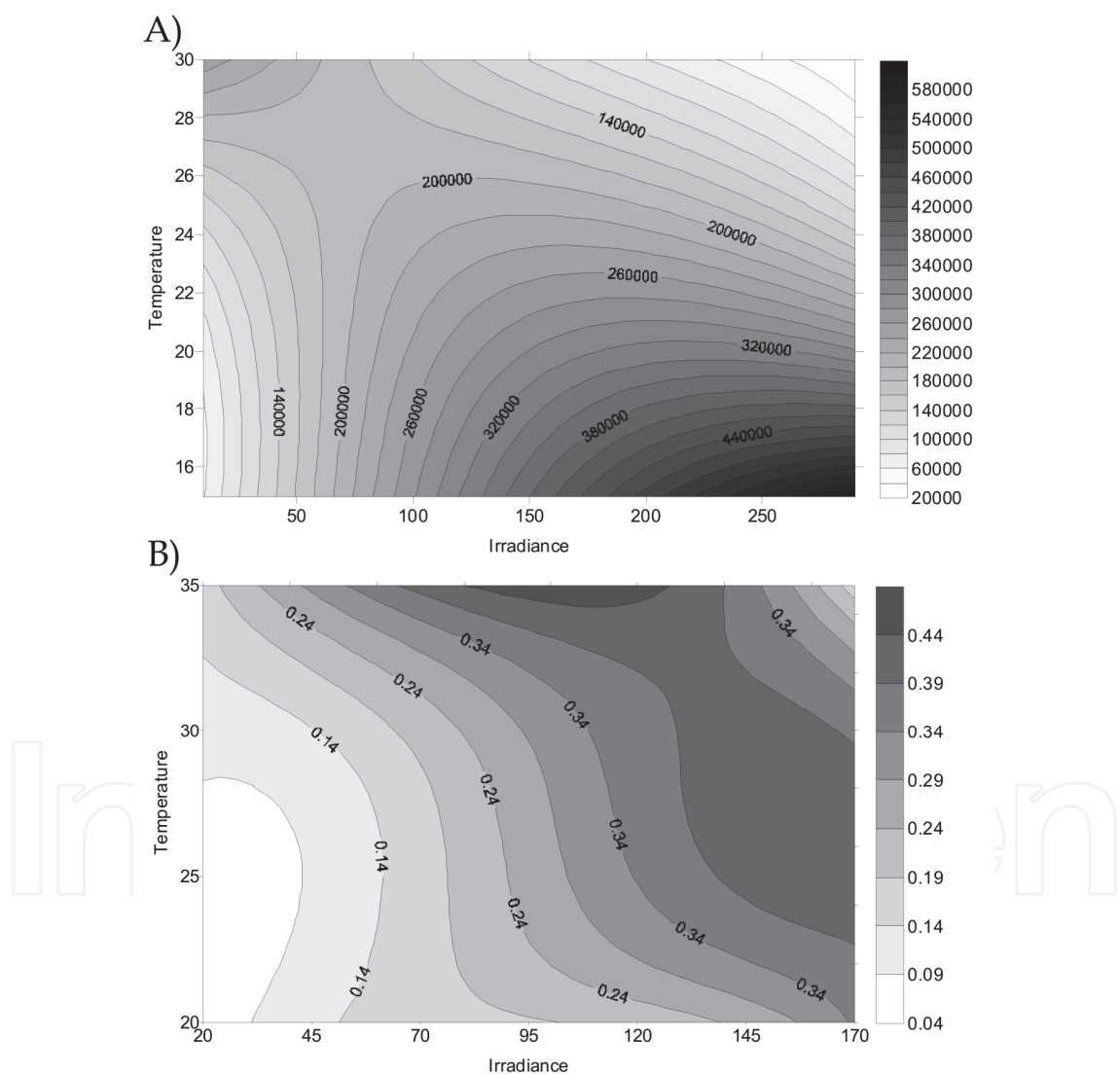


Fig. 1. Response-surface estimation at different temperatures (°C) and irradiances ($\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) of: A) *N. spumigena* filament concentration (1 filament unit = 100 μm), B) *G. amphibium* optical density at 750 nm. Experimental cultures were grown in three replicates and the measurements of culture were done on the last day of incubation in the exponential growth phase.

suggested that photoinhibition of the growth and photosynthesis occurred in the natural populations at above 200 $\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, although a lot of species can be subjected to this phenomenon at lower irradiance. *Aphanizomenon ovalisporum* indicated inhibition of the cell concentration even at 50 $\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and 20-35°C (Hadas et al., 2002). The experiments on *N. spumigena* and *G. amphibium* showed that both irradiance and temperature were important factors contributing to the variation of chlorophyll *a* content at the investigated strains, but the influence of irradiance was higher (Latała & Misiewicz, 2000; Jodłowska & Latała, 2010) (Fig. 2). In two investigated strains, pigment content was negatively affected by irradiance and positively by temperature. The highest values of pigment content at low light treatment and high temperature treatment were almost 95% and 85% for *N. spumigena* and *G. amphibium*, respectively, higher than the lowest ones at high light treatment and low temperature treatment.

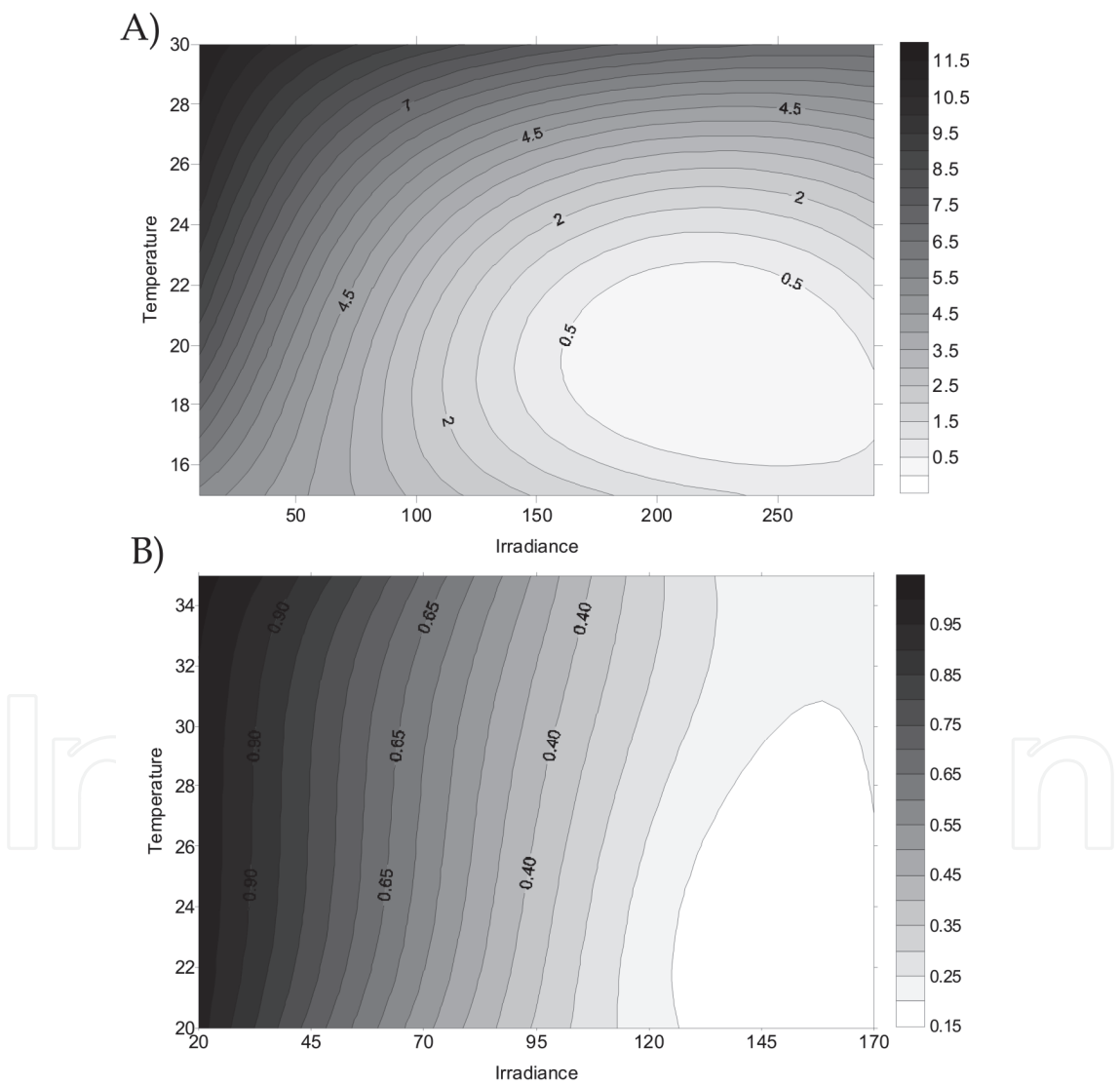


Fig. 2. Response-surface estimation of chlorophyll *a* content (pg filament unit⁻¹): A) *N. spumigena* and B) *G. amphibium* at different temperatures (°C) and irradiances (μmol photons·m⁻²·s⁻¹).

The lower cellular content of chlorophyll *a* noted in the population acclimated to high light is associated with a decrease in the size and/or the number of photosynthetic units (PSUs) that can be reflected by P-E curves (Platt et al., 1980; Prézelin, 1981; Ramus, 1981; Richardson et al., 1983; Henley, 1993; Dring, 1998; Mouget et al., 1999; MacIntyre et al., 2002; Jodłowska & Latała, 2010). P-E curves obtained for *N. spumigena* and *G. amphibium* grown under different light and temperature conditions illustrate that these two strains conform to more than one of the photoadaptive models used to categorize species (Fig. 3) (Jodłowska & Latała, 2010). Photosynthetic rates, normalized to biomass and chlorophyll unit, were plotted against irradiance. The P-E curves were fitted to the data with Statistica using the mathematical function by Platt & Jassby (1976), as follows: $P = P_m \cdot \tanh(\alpha \cdot E / P_m) + R_d$. To illustrate the course of P-E curves, the results recorded at 15°C were chosen (Fig. 3 and 4). In *N. spumigena* culturing at 15°C, the biomass-specific P_m was about 70% higher in the low light treatment than in the high light treatment (Fig. 3A), whereas in *G. amphibium* the same difference was about 60% (Fig. 3B). Since the biomass-specific P_m noted in the strains acclimated to low light was higher than that grown in high light, it indicates a change in the number of the PSUs. However, higher chl*a*-specific P_m in the strains acclimated to high light in comparison to that in the low light strain indicates there was a change in the size of the PSUs. In *N. spumigena* culturing at 15°C, the chlorophyll-specific P_m was about 45% higher in the high light treatment than in the low light treatment (Fig. 3B), whereas in *G. amphibium* the same difference was about 70% (Fig. 4B).

These two mechanisms of photoacclimation, concerning the changes in the size and the number of PSUs, explain significant changes in photosynthesis rate and its parameters upon the influence of different light intensities and temperatures (Fig. 5). It is noteworthy that *N. spumigena* and *G. amphibium* exhibit substantial changes in E_k and P_c within the range of irradiance tested. However, it is typical for E_k values to increase in phototrophic populations as irradiance increases (Richardson et al., 1983), whereas the link between the evolution of compensation light intensity (P_c) and increased irradiance is somewhat more characteristic of Chlorophyta (Falkowski & Owens, 1980). The results of variance analysis showed that both irradiance and temperature were important factors contributing to the variation of E_k and P_c parameters at the investigated strains, but the influence of irradiance was higher. In *N. spumigena*, the minimum values of E_k (about 145 $\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) were about 47% lower than the maximum ones (about 275 $\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) (Fig. 5A), but in *G. amphibium* the differences were higher, and were about 94% (Fig. 5B). In contrast, in cyanobacterium *N. spumigena*, the minimum values of P_c (about 10 $\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) were lower about 95% than the maximum ones (about 180 $\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) (Fig. 5C), whereas in *G. amphibium* the minimum P_c (about 5 $\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) were lower about 93% than the maximum ones (about 70 $\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) (Fig. 5D). The obtained minimum values of E_k and P_c are close to those reported for shadow-tolerant plants, while the maximum ones are close to those noted in heliophyllous plants (Rabinowitch, 1951; Wallentinus, 1978). Achieved results for both parameters showed good acclimation capacity of the investigated species to irradiance changes. It is also noteworthy that P-E curves for investigated cyanobacteria did not indicate photosynthetic photoinhibition until approximately 700-1000 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, even if the cyanobacteria were acclimated to very low light intensity (5 -10 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$). Moisander et al. (2002) did not also note this phenomenon in *N. spumigena* at irradiances exceeding 1000 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$.

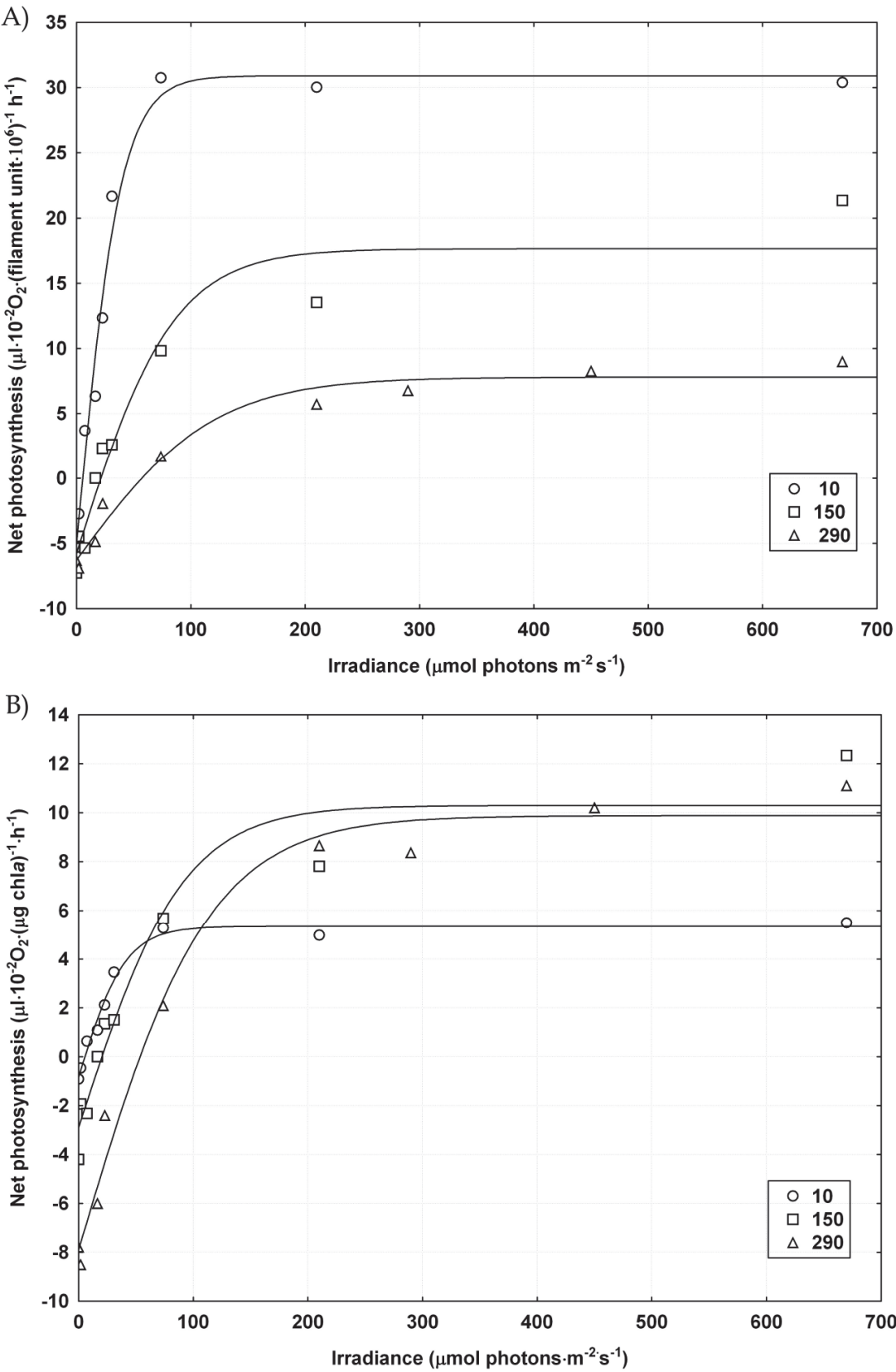


Fig. 3. P-E curves for *N. spumigena* growing at three light intensity ($\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and at 15°C: A) in filament unit, B) in chlorophyll unit (Jodłowska & Latała, 2010).

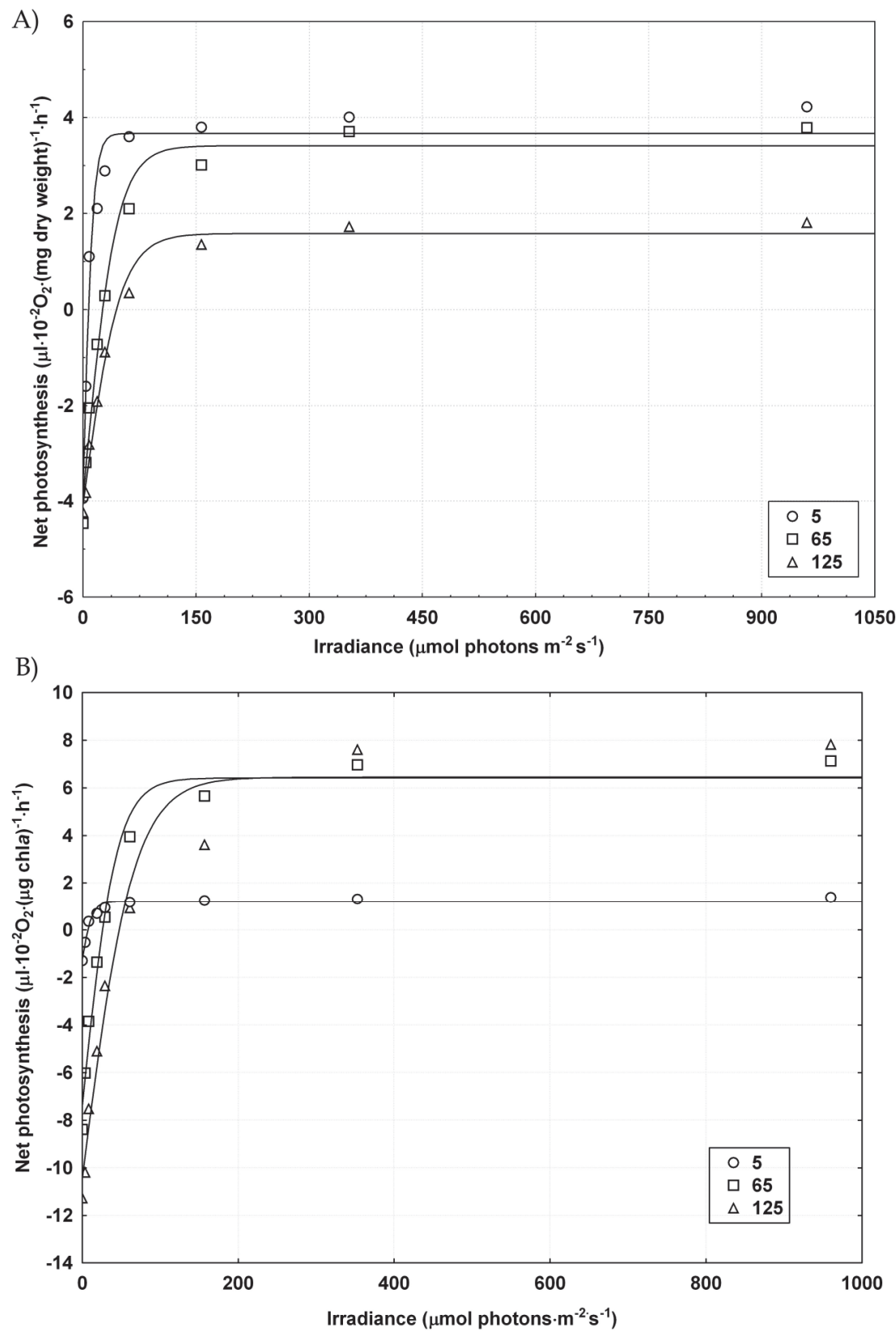


Fig. 4. P-E curves for *G. amphibium* growing at three light intensity ($\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and at 15°C: A) in biomass unit, B) in chlorophyll unit.

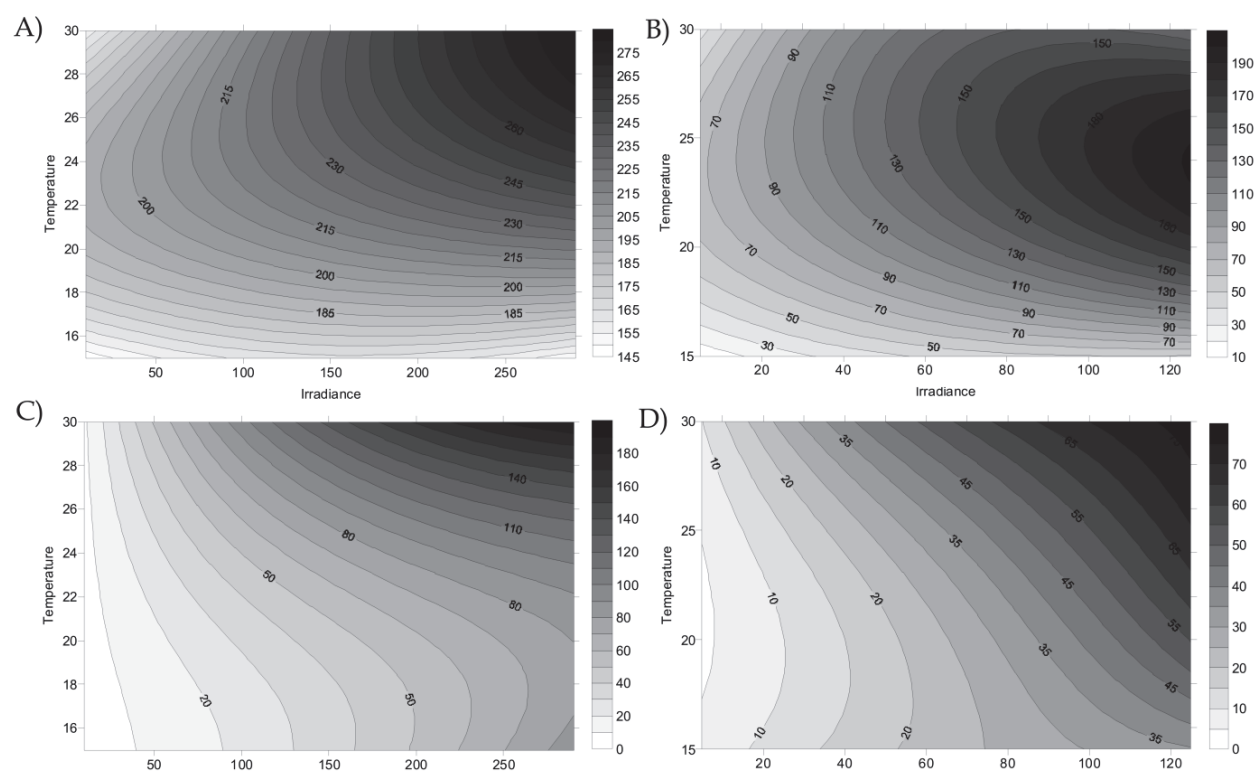


Fig. 5. Response-surface estimation at different temperatures ($^{\circ}\text{C}$) and irradiances ($\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) of E_k ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$) for: A) *N. spumigena*, B) *G. amphibium* and P_c ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$) for: C) *N. spumigena*, D) *G. amphibium*.

5. Conclusions

Every phototrophic organisms, including cyanobacteria, differ in their light intensity range within which they grow and photosynthesize. This is determined by their optimal ecological requirements for light and controlled by metabolic properties of each species (Collier et al., 1978; Richardson et al., 1983). The P-E response curves, derived from short-term measurement, provides an information about condition of photosynthetic apparatus and yields insight into the regulation of energy and material balance of the cell (MacIntyre et al., 2002).

In this review, we give importance of interpreting P-Es in the context photoacclimation mechanisms in cyanobacteria. The current experiments on two different strains of cyanobacteria demonstrated their capacity to acclimate to irradiance, which is reflected in the wide range of changes in the growth, pigment composition as well as photosynthetic activity of the examined cyanobacteria. The studied parameters demonstrated their exceptional adaptability of changes, which explain why these strains grow successfully in well-illuminated habitats and also can grow well in position with limited access of light.

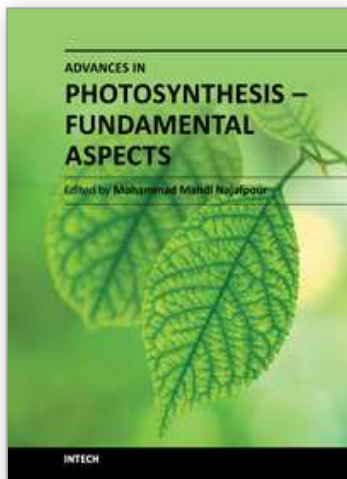
The identification of factors that regulate the growth and photosynthetic activity of cyanobacteria can be helpful for understanding the ecological triggers of cyanobacterial blooms.

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Photosynthesis is one of the most important reactions on Earth. It is a scientific field that is the topic of many research groups. This book is aimed at providing the fundamental aspects of photosynthesis, and the results collected from different research groups. There are three sections in this book: light and photosynthesis, the path of carbon in photosynthesis, and special topics in photosynthesis. In each section important topics in the subject are discussed and (or) reviewed by experts in each book chapter.

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