

BOTANICA LITHUANICA

ISSN 2029-932X

2014, 20(1): 57–63

RESPONSE OF FRESHWATER BLOOM-FORMING PLANKTONIC CYANOBACTERIA TO GLOBAL WARMING AND NUTRIENT INCREASE

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Abstract

Savadova K., 2014: Response of freshwater bloom-forming planktonic cyanobacteria to global warming and nutrient increase [Planktoninių melsvabakterių atsakas į globalinį atšilimą ir maistmedžiagių kiekio padidėjimą gėluose vandens telkiniuose]. – Bot. Lith., 20(1): 57–63.

Human activities stimulate changes in aquatic environment, promoting temperature rise and eutrophication. Disturbance in aquatic ecosystems lead to alterations in plankton communities and food web structure. Cyanobacteria, which are able to regulate their buoyancy, are adapted to low-light, high temperatures, are capable to store phosphorus and fix nitrogen, produce toxins, which help to acquire competitive traits over other phytoplankton species. So, increasing temperature and loadings of nutrients in lakes stimulate successful proliferation of cyanobacteria and heavy bloom formation. Usually higher temperature (> 20°C) and lower N:P mass ratio determine the dominance of cyanobacteria species in lakes and this is expected to increase in the future.

Keywords: cyanobacteria, eutrophication, lakes, nutrients, temperature.

INTRODUCTION

Cyanobacteria are the earliest photosynthetic prokaryotic organisms on the Earth, and are widely distributed from polar to tropical regions in terrestrial and aquatic environments (SCHOPF, 2000). They are primary producers in the water bodies and are considered as an important group among phytoplankton, especially in eutrophic ecosystems. Cyanobacteria are a diverse group, where most of species are slow growing, large-sized K-strategists and reach the highest biomass in temperate regions from July to the mid of September (REYNOLDS, 1984). Cyanobacteria group has exceptional and extremely adaptable ecophysiological features (LITCHMAN et al., 2010) such as ability to develop successfully at higher temperatures, buoyancy regulation using gas vacuoles, capacity to store phosphorus, nitrogen fixation, toxin production, akinete formation, ability to capture light waves even under low light conditions. However, none of the cyanobacteria has all features mentioned previously, so cyanobacteria species composition depends on changes in the environment (CAREY et al., 2012).

Human activities (e.g. industry, agriculture, wetland reclamation, exhaust of gas, etc.) stimulate climate change and promote eutrophication processes in water bodies. Due to greenhouse effect, the rise of air temperature leads to subsequent increase of water temperature. Changes in temperature have become relevant for the alteration in phytoplankton composition because species have their different optimal growth (Nicklisch et al., 2008). Moreover, nutrient supply into aquatic environment promotes eutrophication that result in the increased water body productivity as well as the decreased biodiversity (Peter, 2004). Changes in physico-chemical and light regime parameters of aquatic ecosystems alter phytoplankton taxonomical structure. Phosphorus and nitrogen stimulate cyanobacteria, especially hazardous one, dominance and heavy bloom formation (SMITH, 2003; HAVENS,

2008). Massive proliferations of some species hereby disturb natural trophic chains in freshwaters and also may cause problems of water quality degradation in water bodies important for fishery and recreation (Codd, 2000; VASCONCELOS, 2006; IPCC, 2007).

Numerous investigations are carried out to assess optimal growing conditions and predict proliferation of cyanobacteria in changing conditions (Kokociński et al., 2010; Liu et al., 2011). The current overview is focused on features, which help cyanobacteria co-exist within the group and compete with the other plankton algae as well as on cyanobacteria response to increased temperature and nutrient concentrations.

Global warming effect

During the 20th century, the surface temperature on the Earth raised approximately by 1°C and is still expected to increase from 1.5°C to 5°C during the recent century (Houghton et al., 2001; IPCC, 2007). Cyanobacteria have ability to survive successfully under global warming conditions, because elevated temperatures favour especially surface bloom-forming species, which are adapted to warmer conditions and may reach excessive growth rate at high temperatures (usually > 25°C) (Foy et al., 1976; REYNOLDS, 2006). Under increasing temperature, cyanobacteria overcome eukaryotic algae suppressing their growth in response to warming (JÖHNK et al., 2008; Elliott, 2010; Paerl et al., 2011). The increasing temperature of the atmosphere prolongs the period of stratification (e.g. makes the environment more stable) (LIVINGSTONE, 2003). Many cyanobacteria species prefer stable water column and can regulate their buoyancy using gas vacuoles (Mur et al., 1999). When water stratification occurs in lake, cvanobacteria may change buoyancy regime: float on water surface, where light is available for intensive photosynthesis. During this process, carbohydrates are accumulated in cells, which become heavy and sink to lower water layers, then carbohydrates are used for respiration and the buoyancy of cell restored (VANCE, 1965; Mur et al., 1999). Therefore, cyanobacteria can built up high biomass and out-compete other plankton algae by the light shading.

According to SITOKI et al. (2012), Anabaena (Nostocales) species are susceptible to water column mixing and low light conditions. These genera can be found in both deep and shallow water bod-

ies, under stratification conditions or during quiet summer periods (HAVENS, 2008). Planktothrix is the most commonly bloom forming genus from the order Oscillatoriales, which tolerates wide range of temperatures: from very low (6-16°C) (BERGER, 1989; Dokulil & Teubner, 2000) to those above 20°C (RAMBERG, 1988). So, their blooms may exist all year round, occurring in various water column depths during the season (SIVONEN & JONES, 1999; OBERHAUS et al., 2007). The optimal growth rate for Microcystis (Chroococales) is at $\geq 25^{\circ}$ C (Reynolds, 2006; JÖHNK et al., 2008; PAERL & HUISMAN, 2009) and at very high temperature (≥ 30 °C) they overcome most of cyanobacteria and eukaryotic algae species (Fujiмото & Sudo, 1997). They form larger colonies than Anabaena and due to buoyancy, they reach water surface faster (GIKUMA-NJURU & HECKY, 2005). Microcystis may become more toxic under global warming in freshwater ecosystems (IMAI et al., 2008).

Some Nostocales, e.g. Anabaena bergii Ostenfeld, Aphanizomenon aphanizomenoides (Forti) Hortobágyi & Komárek, Cylindrospermopsis raciborskii (Woloszynska) Seenayya & Subba Raju are considered previously as tropical and subtropical species, have expanded their distribution to temperate zone, as a response to increasing atmosphere temperature (Stüken et al., 2006; Koreivienė & Kasperovičienė, 2011). Invasive C. raciborskii are filamentous cyanobacteria, which can tolerate a wide range of environmental conditions, but temperature is a key factor for this species with the optimal growth rate assessed at 25–35°C (Briand et al., 2004; Castro et al., 2004). Mehnert et al. (2010) showed that invasive species such as Aphanizomenon ovalisporum Forti, A. aphanizomenoides and Cylindrospermopsis raciborskii have higher growth rate than native cyanobacteria species, if the temperature increases in temperate lakes. They concluded that seasonal development of nostocalean cyanobacteria will be prolonged with the ongoing climate warming and native species such as Aphanizomenon gracile (Lemmermann) Lemmermann will be out-competed by new invaders such as Cylindrospermopsis raciborskii. Invasive species show preference to occur in polymictic shallow lakes (STÜKEN et al., 2006), but also may be found in stratified lakes, where they coexist with native cyanobacteria (MISCHKE & NIXDORF, 2003; RÜCKER et al., 2007).

Nutrient increase effect

In temperate climate zone, cyanobacteria occur from mesotrophic to eutrophic (Cerasino & Salmaso, 2012) and are more common in highly productive lakes (Kasperovičienė et al., 2005; Eldridge et al., 2012). Cyanobacteria amount and species composition have seasonal pattern of variation. Species diversity tends to be higher in early summer than late summer under intensive cyanobacteria proliferation (Sze, 1986). The variation of environmental conditions during vegetation period is a key factor determining cyanobacteria species.

Commonly under lower N:P ratio cyanobacteria become dominant, this is due to the fact that this group has more competitive traits for nitrogen than other plankton species, as many cyanobacteria could form heterocysts and fix nitrogen (Huisman & HULOT, 2005). For example, planktonic species of the nostocalean cyanobacteria genera such as Anabaena and Aphanizomenon become diazotrophic at scarce inorganic nitrogen conditions (CHAN et al., 2004; HAVENS, 2008; Wood et al., 2010), commonly form heavy blooms worldwide. Anabaena and Aphanizomenon usually form blooms in moderately deep, stratified and eutrophic lakes (PAERL et al., 2001). According to Nõges et al. (2008), in shallow lake nitrogen fixation starts at decreased TN:TP mass ratio till it reaches about 20. Domingues et al. (2005) demonstrated that lower N:P values and higher temperature initiate succession from green algae species to nitrogen fixing cyanobacteria (e.g. Anabaena).

Some other studies showed that nutrient concentrations, especially P, are more important as cyanobacteria are poor competitors for phosphorus (Nõges et al., 2003). However, some freshwater cyanobacteria have ability to deal with variable P concentrations, because species have the storage capacity for phosphorus (Mur et al., 1999: Dyhrman et al., 2007). For example, Cylindrospermopsis raciborskii was noted as strong competitor under phosphate shortage (Istvànovics et al., 2000; Posselt et al., 2009). Other authors claim that C. raciborski usually is typical at high TN:TP ratios (Briand et al., 2002). Harmful cyanobacteria blooms could be stimulated in N-enriched waters (at high N:P) (PAERL & FUL-TON, 2006), especially for non-nitrogen fixing genera (Microcystis, Planktothrix, Raphidiopsis, Woronichinia) species (Galloway et al., 2002). Non-nitrogen fixing cyanobacteria (e.g. genus Microcystis) prefer N-NH₄ rather than N-NO₂ as nitrogen source (Blomovist et al., 1994). On the other hand, Liu et al. (2011) investigations showed that Microcystis biomass proportion increased with decreasing TN:TP mass ratio from 44 (in April formed 10.6%) to 24.2 (in July formed 49.3%), so Microcystis dominated under low TN:TP ratio (< 30) and warm temperature. Fuлмото & Sudo (1997) also got consistent conclusion during the experiment that non-diazotrophic Microcystis dominated at low N:P ratio < 44. According to O'Neil et al. (2012), the density and/or toxicity of Microcystis bloom depend on the phosphorus loadings. Planktothrix agardhii benefits at raised phosphorus concentrations (low TN:TP) (RÜCKER et al., 1997: Kokociński et al., 2010), but P. rubescens (De Candolle ex Gomont) Anagnostidis & Komárek was found in oligotrophic lakes, as nutrients aren't the key factor (JACQUET et al., 2005; LEGNANI et al., 2005; Ernst et al., 2009). Limnotrix redekei and P. agardhii often occur in shallow and eutrophic lakes of temperate zone and compete successfully with the other filamentous cyanobacteria (Rücker et al., 1997; Kokociński et al., 2010).

In conclusion, it should be said that surface temperature on the Earth is still expected to increase (IPCC, 2007). Cyanobacteria have numerous adaptable traits that help them to reach higher growth rates at elevated temperatures (e.g. ≥ 20°C) over the other eukaryotic plankton algae species (PEPERZAK, 2003; PAERL & HUISMAN, 2009). Thus, the dominance of cyanobacteria as well as increased frequency and duration of their blooms may be expected more often worldwide. Also, this may favour the distribution of cyanobacteria species from tropical and subtropical regions into the lakes of temperate regions, altering plankton communities structure and disturbing natural lake ecosystems. Previously discussed studies showed that commonly cyanobacteria successfully proliferate at lower N:P mass ratio for both nitrogen and non-nitrogen fixing species. It is noticeable that eutrophic lakes are characterized by lower N:P ratio, that is why cyanobacteria usually dominate in phytoplankton assemblages of eutrophic and hypertrophic lakes (SMITH, 1983; PAUL, 2008; LIU et al., 2011). So, anthropogenic nutrient pollution play on one hand with the increased temperature promoting cyanobacteria proliferation, and the particular concentrations of nutrient ratio decide interspecific competition between algae.

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PLANKTONINIŲ MELSVABAKTERIŲ ATSAKAS Į GLOBALINĮ ATŠILIMĄ IR MAISTO MEDŽIAGŲ KIEKIO PADIDĖJIMĄ GĖLUOSE VANDENS TELKINIUOSE

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Santrauka

Žmogaus veikla sukelia aplinkos sąlygų pasikeitimus, kurie skatina vandens telkinių temperatūros didėjimą ir eutrofikacijos procesą, tai lemia pokyčius vykstančius vandens ekosistemų fitoplanktono struktūroje ir mitybos grandinėse. Melsvabakterės geba reguliuoti plūdrumą, prisitaikyti prie silpno apšvietimo, aukštos temperatūros, turi gebėjimą kaupti fosforą ir fiksuoti azotą, gaminti toksinus, todėl kintančiomis aplinkos sąlygomis yra pranašesnės kon-

kurencinėje kovoje lyginant su kitomis fitoplanktono rūšimis. Taigi, didėjanti temperatūra ir vykstanti intensyvi apkrova maisto medžiagomis lemia sėkmingą melsvabakterių vystymąsi ir vandens žydėjimo formavimą ežeruose. Dažniausiai aukštesnė temperatūra (> 20°C) ir mažesnės N:P santykio reikšmės nulemia melsvabakterių dominavimą ežeruose ir ateityje šis reiškinys stiprės dėka vis labiau besikeičiančių aplinkos sąlygų.