

Annales Universitatis Paedagogicae Cracoviensis Studia Naturae, 2: 114–123, ISSN 2543-8832 DOI: 10.24917/25438832.2.9

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Allelopathic effect of the Baltic picocyanobacterium *Synechococcus* sp. on selected diatoms

Introduction

The allelopathy phenomenon was originally defined as a harmful effect between plants. This definition was used for the first time by Professor Hans Molisch (1937). As the result of the development of science and a better understanding of this phenomenon, the definition of allelopathy has evolved. The International Allelopathy Society (IAS, 1996) established the definition of allelopathy as the process in which the compounds secreted by different organism (vascular plant, algae, bacteria and fungi) influenced the growth and development of the both plant and animal organisms (Legrand et al., 2003). These chemical substances were called allelopathic compounds or allelochemicals (Leflaive, Ten-Hage, 2007), and organisms used them to protection against predators, and avoid competitors (Granéli et al., 2008).

In aquatic ecosystems, allelopathic interactions are still not very well recognised, because the distance between organisms which are able to secreting secondary metabolites is crucial to observe the allelopathic effect (Wolfe, 2000). Allelopathy in freshwater, brackish, and marine ecosystems depends on the production and secretion of active allelopathic compounds and their effective spread to other organisms (Lewis, 1986). Therefore, to demonstrate allelopathy between photoautotrophs, scientists need to perform a number of laboratory experiments.

It has been proven that several groups of phytoplankton, such as cyanobacteria, dinoflagellates, prymnesiophytes, green algae, and diatoms product allelopathic compounds (Subba Rao, Smith, 1995; Chiang et al., 2004; Żak, Kosakowska, 2015). Moreover, published data indicated that allelopathic effects have the competitive advantage of some phytoplankton species by eliminating physiologically more sensitive species (Sarkar et al., 2006). Moreover, the structure of phytoplankton (Legrand et al., 2003) and the formation of cyanobacterial and algal blooms may be determined by allelopathic interactions (Smayda, 1997; Weissbach et al., 2010). Massive and harmful cyanobacterial and algal blooms are a serious problem affecting not only the ecology but also the economy of the aquatic ecosystem (Anderson, 1989; Anderson et al., 2002). Massive blooms are formed by cyanobacteria (also picocyanobacteria from the genus *Synechococcus*), green algae, dinoflagellates, and diatoms (Beardall, 2008; Błaszczyk et al., 2010).

Little is known about the influence of cyanobacteria on diatoms (Sivonen, Jones 1999), and the specific mechanism of action of the allelopathic interactions is unexamined. It is impossible to demonstrate allelopathy in natural conditions, which is why it is important to contribute controlled experiments in laboratory environment. Therefore, in this study, we investigated the allelopathic effect of picocyanobacterium *Synechococcus* sp. on diatoms *Nitzschia fonticola* (Grunow) Grunow, *Fistulifera saprophila* (Lange-Bertalot & Bonik) Lange-Bertalot, *Navicula perminuta* Grunow and *Amphora coffeaeformis* (C.Agardh) Kützing. In this study, the influence of picocyanobacteria was examined by adding the cell-free filtrate of *Synechococcus* sp. to studied diatoms. The results of this experiment may provide further information about allelopathic interactions between cyanobacteria and diatoms, which could be important to the understanding of cyanobacterial and algal blooms in aquatic ecosystems, including the Baltic Sea.

Material and methods

The experiments were conducted on the strain of picocyanobacterium Synechococcus sp. (BA-124) and four diatoms: Nitzschia fonticola (BA-34), Fistulifera saprophila (BA-56), Navicula perminuta (BA-30), and Amphora coffeaeformis (BA-16) (Fig. 1). These species are typical representatives of Baltic diatoms; therefore, they were selected for the allelopathic experiment. The strains were isolated from the coastal zone of the Gulf of Gdańsk (southern Baltic Sea) and are maintained as uni-algal cultures in the Culture Collection of Baltic Algae (CCBA) at the Institute of Oceanography, University of Gdańsk, Poland (Latała et al., 2006). The tests on the 'batch cultures' were carried out in 25 mL glass Erlenmeyer flasks containing sterilised f/2 medium (Guillard, 1975). The media were prepared from Baltic water, which was filtered through Whatman GF/C glass fibre filters, and autoclaved. Analysed organisms were grown 7 days in constant conditions of 18°C and 8 psu, under a 16:8 h light : dark cycle at 10 µmol photons·m⁻² s⁻¹ and this were the control treatment conditions. Fluorescent lamps (Cool White 40W, Sylvania, USA) were used as source of irradiance. The intensity of PAR was measured using a LI-COR quantum-meter with a cosine collector. The donor and target organisms were acclimated to these culture conditions for 7 days; afterwards, actively growing cultures were used for the establishment of the allelopathic experiment.

Allelopathic interactions in monocultures were determined by using the modified method proposed by Suikkanen et al. (2004). Allelopathic interaction



Fig. 1. Diatoms strains used in this study: *Nitzschia fonticola* (A), *Fistulifera saprophila* (B), *Navicula perminuta* (C) and *Amphora coffeaeformis* (D); scale bars = 10 µm

was studied by adding the filtrate obtained from the picocyanobacterial culture of *Synechococcus* sp. BA-124 to tested diatoms. The culture of picocyanobacteria was filtered through 0.45-µm pore size Macherey-Nagel MN GF-5 filters. The cellfree filtrate (V = 10 mL) was added to 25 mL Erlenmeyer flasks containing the tested diatoms (V = 10 mL). In all experiments, the ratio of picocyanobacterium to target species in Erlenmeyer flasks was adjusted to 1:1, based on the chlorophyll *a* content (final chlorophyll *a* concentration in the experimental cultures was 0.4 µg chl *a* mL⁻¹). Control samples were prepared by adding mineral medium f/2 with a volume equal to the added cell-free filtrate. Tests were conducted in triplicate, and all analysed species were obtained from early exponential growth phase.

The number of cells was counted using flow cytometer BD Accuri^{**} C6 Plus. Events are recorded in list mode. To avoid generating large files, samples can be run for 40s at a delivery rate of 14 μ l·min⁻¹, and the number of events is kept at less than 1000 per second. Events are recorded in standard filters: 670 LP (Detector FL3) and 675/25 (Detector FL4) (Marie et al., 2005). The number of cells in the experimental cultures was determined after the 1st and 7th day of the diatoms exposure to the picocyanobacterial filtrate.



Fig. 2. The effect of the addition of cell-free filtrate from Synechococcus sp. BA-124 cultures on the growth of *Nitzschia fonticola* (A), *Fistulifera saprophila* (B), *Navicula perminuta* (C) and *Amphora coffeaeformis* (D) after the 1st and 7th days of exposition, expressed as a number of cells (N). The values refer to means (n = 3, mean \pm SD); asterisk indicates significant difference compared with control (p < 0.05)

Chlorophyll *a* fluorescence was measured with a Pulse Amplitude Modulation (PAM) fluorometer (FMS1, Hansatech), using a 594 nm amber modulating beam with 4 step frequency control as a measuring light. Analysed species were taken for chlorophyll fluorescence analysis after the 7th day of exposure to the filtrate. Before measurements, each sample taken from the culture was filtered through 13 mm glass fibre filters (Whatman GF/C). Before starting the experiment, the filter sample was adapted in the dark for about 10 minutes. The maximum quantum yield of PSII photochemistry (F_v/F_m) and effective quantum yield of PSII photochemistry (Φ PSII) was calculated (Campbell et al., 1998).

Analysis of variance (one-way ANOVA) was used to test for differences in analysed parameters between the target cultures treated with picocyanobacterial cellfree filtrates and the control over the experimental period. Data are reported as mean \pm standard deviation (SD). Levels of significance were * p < 0.05. The statistical analyses were performed using the Statistica^{*} 13.1 software.

Results

The effect of the cell-free filtrate addition obtained from *Synechococcus* sp. cultures on the growth of analysed diatoms *Nitzschia fonticola*, *Fistulifera saprophila*, *Navicula perminuta* and *Amphora coffeaeformis* after 1 and 7 days of exposition to the filtrates



Fig. 3. The effect of the addition of cell-free filtrate from Synechococcus sp. BA-124 cultures on the fluorescence parameters F_v/F_m and Φ PSII of *Nitzschia fonticola* (A), *Fistulifera saprophila* (B), *Navicula perminuta* (C) and *Amphora coffeaeformis* (D) after the 7th day of exposition; the values refer to means (n = 3, mean ± SD); asterisk indicates significant difference compared with control (p < 0.05)

are shown in figure 2. The results showed that addition of cell-free filtrate from *Synechococcus* sp. increased the number of cells of *N. fonticola* and *F. saprophila* compared to their control. After the 7th day of the experiment for a filtrate addition, growth stimulation of *N. fonticola* and *F. saprophila* constituted 105% and 107%, respectively (ANOVA, p < 0.05). In addition, it was observed that the cell-free filtrate obtained from picocyanobacterium did not affect the number of cells of *N. perminuta* and *A. coffeaeformis* (ANOVA, p > 0.05).

The effect of the addition of cell-free filtrate from *Synechococcus* sp. cultures on the fluorescence parameters F_v/F_m and Φ PSII of analysed diatoms after one week of exposition is showed in figure 3. The study indicated that the addition of cell-free filtrate obtained from *Synechococcus* sp. significantly affected the F_v/F_m and Φ PSII of *N. fonticola* and *N. perminuta*. After the 7th day of exposition, it was noted that the addition of the filtrate resulted in increase of fluorescence parameters of analysed diatoms, which was higher by 29% and 4%, respectively, for F_v/F_m and 56% and 14%, respectively for Φ PSII, compared to a control (ANOVA, p < 0.05). Based on the results, it was found that the filtrate obtained from *Synechococcus* sp. also caused significant changes of the Φ PSII value of *F. saprophila*. After one week of the experiment, the fluorescence parameter of this diatom was higher by 6%, compared to control (ANOVA, p < 0.05). On the other hand, it was noted that filtrate obtained from picocyanobacterium caused the inhibition of the F_v/F_m parameter of *A. coffeaeformis*, which constituted 96% (ANOVA, p < 0.05).

It is believed that cyanobacterial allelopathy may be one of the important factors affecting the formation of massive algal blooms in the aquatic ecosystems (e.g., Antunes et al., 2012; Rzymski et al., 2014). Picocyanobacteria plays an important role in aquatic ecosystems but not much is known about their allelopathic activity. Therefore, the main aim of this study was to investigate the allelopathic effect of picocyanobacterium *Synechococcus* sp. on growth and fluorescence parameters of *Nitzschia fonticola*, *Fistulifera saprophila*, *Navicula perminuta*, and *Amphora coffeaeformis*.

Allelopathic effects of the growth of the target organism by the production allelopathic compounds are the most frequently reported mode of the action of cyanobacteria and microalgae (Rzymski et al., 2014). In this study, we have also demonstrated that picocyanobacterium caused allelopathic effects against Baltic diatoms. The results showed that addition of cell-free filtrate from Synechococcus sp. increased the number of cells of N. fonticola and F. saprophila. In addition, it was observed that the cell-free filtrate obtained from picocyanobacterium did not affect the number of cells of N. perminuta and A. coffeaeformis. Only a few studies have documented the influence of the allelopathic effect of cyanobacteria on diatoms species. Information about the allelopathic interactions of Synechococcus sp. on Baltic diatom N. preminuta was described by Śliwińska-Wilczewska et al. (2016). In this study, the authors demonstrated that the addition of the cell-free filtrate obtained from the picocyanobacterium had an inhibitory effect on analysed diatom. Moreover, the study reveals that allelopathic activity was regulated by the intensity of light, temperature, and salinity. Keating (1977, 1978) also demonstrated the growth inhibition of selected diatom by the addition of filtrate obtained from a lake in which cyanobacteria was dominated. Similar results were reported by Lafforgue et al. (1995), who showed that the low biomass of Fragilaria crotonensis Kitton in Lake Aydat was the result of the allelochemicals obtained from Anabaena sp. More detailed data on the allelopathic effects of Baltic cyanobacteria on diatoms were provided by Suikkanen et al. (2004). In this study, the allelopathic effects of Baltic Nodularia spumigena Mertens ex Bornet & Flahault, Anabaena lemmermannii P.G.Richter and Aphanizomenon flosaquae Ralfs ex Bornet & Flahault on the diatom Thalassiosira weissflogii (Grunow) G.Fryxell & Hasle were demonstrated. The authors showed that, after a single addition of the filtrate, all three analysed cyanobacteria had a generally negative effect on the tested diatom. Moreover, on the basis of the research, it was noted that the diatom of T. weissflogii showed some tolerance for a single addition of the filtrate, but its growth after repeated additions of the filtrate was significantly inhibited. Different characteristics, such as membrane permeability, may contribute to the sensitivity of some phytoplankton species to allelopathic compounds (Suikkanen et al., 2004). The sensitivity of organisms may also depend on the nature of allelopathic compounds to which they are exposed, because the same target organisms may react differently to the filtrate derived from different donor organisms.

There are also only a few reports on the growth stimulation of target organisms caused by allelochemicals produced by cyanobacteria. Suikkanen et al. (2005) showed that some Baltic cyanobacteria may stimulate natural plankton communities. The authors found that the addition of *N. spumigena* filtrate significantly increased the numbers of cells of *N. spumigena* and *Anabaena* sp. In our study, allelochemicals produced by *Synechococcus* sp. had the stimulatory effects on the growth of diatoms *N. fonticola* and *F. saprophila*. This indicated that the picocyanobacteria released some compounds that accelerated the growth of selected and co-existing diatoms.

Another possible effect of allelopathic compounds is their effect on the photosynthetic activity of target organisms. Measurements of chlorophyll a fluorescence are non-invasive methods. Moreover, fluorescence measurements are a useful tool in the study of the allelopathy and ecophysiology of cyanobacteria and microalgae (Prince et al., 2008). In this study, it was found that the addition of filtrate stimulated and inhibited the fluorescence parameters F_y/F_m and $\Phi PSII$ of analysed diatoms. Published data indicated that the allelopathic compounds produced and released by some cyanobacteria can affect the photosynthesis, and detailed studies have shown that they act mainly on the photosystem II (PSII). Issa (1999) presented the inhibitory effect of the donor Oscillatoria sp. and Calothrix sp. on photosynthesis of Chlorella fusca Shihira & R.W.Krauss. More detailed studies were conducted Prince et al. (2008). The authors analysed the impact of Karenia brevis (C.C.Davis) Gert Hansen & Ø.Moestrup on fluorescence parameter F_v/F_m of target diatoms Amphora sp., Asterionellopsis glacialis (Castracane) Round and Skeletonema costatum (Greville) Cleve. Inhibition of photosynthetic yield by extract obtained from K. brevis coincided with a negative effect on the growth of target organisms. The effect of allelopathic compounds may be due to the different sensitivity of the target species (Mulderij et al., 2003), and this may explained the dominance of some species over other photoautotrophs.

It is believed that selective stimulation or inhibition of the target organism may affect the succession of selected cyanobacteria and microalgae in aquatic ecosystem (Legrand et al., 2003). The present research demonstrated the allelopathic effect of *Synechococcus* sp. either inhibited or stimulated the growth and fluorescence parameters of selected Baltic diatoms. To evaluate the significance of the picocyanobacterial allelopathy, more detailed studies are needed. These results showed that *Synechococcus* sp. allelopathy should be considered when estimating the potential interactions between picocyanobacteria and diatoms in aquatic ecosystems.

Acknowledgements

The authors would like to thank the anonymous reviewers for their valuable comments and suggestions to improve the quality of the paper. This study was supported by BMN grants, Poland, no. 538-G245-B568-17.

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Abstract

It is commonly believed that the structure of phytoplankton and the formation of cyanobacterial and algal blooms may be explained by allelopathic interactions. The main aim of this study was to investigate the allelopathic effect of picocyanobacterium *Synechococcus* sp. on the following growth and fluorescence parameters: the maximum quantum yield of PSII photochemistry (F_v/F_m), and the effective quantum yield of PSII photochemistry (Φ PSII) of selected diatoms – *Nitzschia fonticola, Fistulifera saprophila, Navicula perminuta* and *Amphora coffeaeformis*. In this study, it was demonstrated that picocyanobacterium caused allelopathic

effects against Baltic diatoms. The results showed that the addition of cell-free filtrate from *Synechococcus* sp. increased the number of cells of *N. fonticola* and *F. saprophila*. Moreover, it was found that picocyanobacterium was stimulated fluorescence parameters of *N. fonticola*, *F. saprophila*, and *N. perminuta*. On the other hand, it was noted that filtrate obtained from picocyanobacterium caused the inhibition of F_v/F_m parameter of *A. coffeaeformis*. The results of this experiment may provide further information about allelopathic interactions between Baltic picocyanobacteria and diatoms that are crucial to the understanding of algal blooms in aquatic ecosystems.

Key words: allelopathy, Baltic Sea, diatom, growth, fluorescence, picocyanobacteria

Received: [2017.07.22] Accepted: [2017.10.27]

Zjawisko oddziaływania allelopatycznego bałtyckiej pikoplanktonowej sinicy *Synechococcus* sp. na wybrane gatunki okrzemek

Streszczenie

Powszechnie uważa się, że oddziaływanie allelopatyczne może mieć wpływ na strukturę fitoplanktonu oraz tworzenie masowych zakwitów sinic oraz mikroglonów. Głównym celem niniejszych badań było wykazanie oddziaływania allelopatycznego pikoplanktonowej sinicy *Synechococcus* sp. na wzrost oraz parametry fluorescencji, charakteryzujące maksymalną wydajność fotosystemu II (F_v/F_m) oraz rzeczywistą wydajność fotosystemu II na świetle (Φ PSII) wybranych gatunków okrzemek: *Nitzschia fonticola, Fistulifera saprophila, Navicula perminuta* i *Amphora coffeaeformis.* Zaobserwowano, że pikoplanktonowa sinica wykazywała alelopatyczne właściwości na badane bałtyckie okrzemki. Na podstawie uzyskanych danych zanotowano, że dodanie przesączu z sinicy *Synechococcus* sp. stymulowało wzrost *N. fonticola* i *F. saprophila.* Ponadto zaobserwowano znaczący wzrost parametrów fluorescencji u *N. fonticola, F. saprophila*. W pracy również wykazano, że przesącz powodował obniżenie wartości parametru F_v/F_m u.*A. coffeaeformis.* Wyniki uzyskane w niniejszej pracy dostarczają szerszych informacji odnoście oddziaływania allelopatycznego, występującego pomiędzy wybranymi gatunkami sinic i okrzemek, które w znaczący sposób mogą przyczynić się do zrozumienia pojawiających się w wielu ekosystemach wodnych masowych zakwitów sinic i mikroglonów.

Słowa kluczowe: allelopatia, Morze Bałtyckie, okrzemki, wzrost, fluorescencja, pikoplanktonowe sinice

Information on the authors

Zofia Konarzewska

The field of her interest is allelopathic interactions of picocyanobacterium *Synechococcus* sp. and Baltic diatoms in monocultures. In her studies, she uses flow cytometer and PAM fluorymetry to determine allelopathic interactions between picocyanobacteria and selected diatoms – *Nitzschia fonticola, Fistulifera saprophila, Navicula perminuta* and *Amphora coffeaeformis*.

Sylwia Śliwińska-Wilczewska

In her research, she is interested in the allelopathy of cyanobacteria and microalgae, and particularly picocyanobacteria *Synechococcus* sp. Allelopathy plays an important role in interspecific competition and contributes to cyanobacterial bloom maintenance. In her study, the influences of allelochemicals on the growth, chlorophyll fluorescence, and photosynthesis irradiance curves of different phytoplankton species were investigated. She is also investigating what influences environmental factors have on produced allelopathic compounds on algae and cyanobacteria.

Adam Latała

His subjects of research include wide experience in the ecophysiology and ecotoxicology of marine benthic and planktonic algae, the influence of the main environmental factors such as salinity, temperature, and light on the photosynthesis, photoacclimation, fluorescence, respiration, and growth of algae from natural communities and cultured under laboratory conditions, and the use of fluorescence techniques to study algal and cyanobacterial ecophysiology and ecotoxicology.