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Research paper

The dinoflagellate *Akashiwo sanguinea* will benefit from future climate change: The interactive effects of ocean acidification, warming and high irradiance on photophysiology and hemolytic activity

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ABSTRACT

Due to global climate change, marine phytoplankton will likely experience low pH (ocean acidification), high temperatures and high irradiance in the future. Here, this work report the results of a batch culture experiment conducted to study the interactive effects of elevated CO_2, increased temperature and high irradiance on the harmful dinoflagellate *Akashiwo sanguinea*, isolated at Dongtou Island, Eastern China Sea. The *A. sanguinea* cells were acclimated in high CO_2 condition for about three months before testing the responses of cells to a full factorial matrix experimentation during a 7-day period. This study measured the variation in physiological parameters and hemolytic activity in 8 treatments, representing full factorial combinations of 2 levels each of exposure to CO_2 (400 and 1000 μatm), temperature (20 and 28 °C) and irradiance (50 and 200 μmol photons m^{-2} s^{-1}). Sustained growth of *A. sanguinea* occurred in all treatments, but high CO_2 (HC) stimulated faster growth than low CO_2 (LC). The pigments (chlorophyll a and carotenoid) decreased in all HC treatments. The quantum yield (F_v/F_m) declined slightly in all high-temperature (HT) treatments. High irradiance (HL) induced the accumulation of ultraviolet-absorbing compounds (UV_{abc}) irrespective of temperature and CO_2. The hemolytic activity in the LC treatments, however, declined when exposed to HT and HL, but HC alleviated the adverse effects of HT and HL on hemolytic activity. All HC and HL conditions and the combinations of high temperature*high light (HTHL) and high CO_2*high temperature*high light (HCHTHL) positively affected the growth in comparison to the low CO_2*low temperature*low light (LCLTLL) treatment. High temperature (HT), high light (HL) and a combination of HT*HL, however, negatively impacted hemolytic activity. CO_2 was the main factor that affected the growth and hemolytic activity. There were no significant interactive effects of CO_2*temperature*irradiance on growth, pigment, F_v/F_m or hemolytic activity, but there were effects on P_m, α, and E_k. If these results are extrapolated to the natural environment, it can be hypothesized that *A. sanguinea* cells will benefit from the combination of ocean acidification, warming, and high irradiance that are likely to occur under future climate change. It is assumed that faster growth and higher hemolytic activity and UV_{abc} of this species will occur under future conditions compared with those the current CO_2 (400 μatm) and temperature (20 °C) conditions.

1. Introduction

Harmful algal blooms (HAB) have occurred around the world at increasing frequencies in recent years and have caused severe and unfavorable consequences to ecosystems and public health under climate change. The responses of HAB to global climate change, e.g., ocean acidification (OA), warming, solar irradiance and nutrients, have been reviewed by several researchers (Chen et al., 2017; Guan and Li, 2017; Xu et al., 2012; Fu et al., 2008, 2012; Gao et al., 2012a; Hallegraeff, 2010; Heiden et al., 2016; Mackey et al., 2015; Mostofa et al., 2016; Shi et al., 2015; Tatters et al., 2013; Van de Waal et al., 2014; Wells et al., 2015). Although the ecological consequences of climate change are likely profound, they are uncertain if multiple stressors or factors are considered, such as warming, solar radiation and nutrient stoichiometry.

Ocean acidification (OA) has become a serious issue to the environment because of its detrimental effects on the balance of

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the carbonate system in the ocean and the marine biogeochemical and ecological processes (Andersson et al., 2003; Feely et al., 2004). As previously reported, high CO_2 can influence the physiology and toxicity of HAB species (Fu et al., 2012; Gao et al., 2012a; Wells et al., 2015), but results among publications are contradictory. Ocean acidification has been found to have positive (Chen et al., 2015a; Errera et al., 2014; Flores-Moya et al., 2012; Hattenrath-Lehmann et al., 2015; Tatters et al., 2013), negative (Eberlein et al., 2016; Van de Waal et al., 2014) and even neutral effects (Fu et al., 2008; Li et al., 2012a; Van de Waal et al., 2014) on the physiological responses of microalgae. These differences were found because the net effects of OA on HAB are largely dependent on the species-specificity (Fu et al., 2007) and other photobiological conditions, e.g., light availability, rising temperatures and nutrient availability, as reviewed by Gao et al. (2012a). For the combined effects of OA and irradiance, Southern Ocean diatoms (*Fragilariopsis curta* and *Odontella weissflogii*) were found to be sensitive to changes in CO_2 and showed species-specific responses, which were further modulated by light intensity (Heiden et al., 2016). Gao et al. (2012b) reported that low to moderate levels of photosynthetically active radiation (PAR) enhanced photosynthesis or growth of phytoplankton, but excessive levels of PAR resulted in the inhibition of photosynthesis or growth under OA. Simultaneously, the response of phytoplankton to the interactive effects of OA and warming were shown to be species specific. Both OA and warming (4 °C increase) were found to promote the growth of *Synechococcus* but not *Prochlorococcus* (Fu et al., 2007). No synergistic effects were found between OA and warming on *Trichodesmium* (Hutchins et al., 2007).

The toxicity of HAB species was also found to be ambiguous in response to OA, which was reviewed by other researchers (Fu et al., 2012; Mackey et al., 2015; Wells et al., 2015). The question of whether OA promotes the growth and toxicity of harmful algae is still open, as the effect of elevated CO_2 concentrations on HAB can be influenced by nutrient stoichiometry, temperature and light conditions. Increased domoic acid (DA) content in *Pseudo-nitzschia fraudulenta* (*P. fraudulenta*) and *Pseudo-nitzschia multiseries* (*P. multiseries*) is stimulated by high CO_2 concentrations under silica (Tatters et al., 2012) and phosphorus limitations (Sun et al., 2011), respectively. Nitrogen (N) or phosphorous (P) limitation also increased the toxicity of *Alexandrium fundyense* (*A. fundyense*), *Scrippsiella trochoidea* (Eberlein et al., 2016) and *Karlodinium veneficum* (Fu et al., 2010) under high CO_2 concentrations. While toxin concentrations (saxitoxin) in *Alexandrium catenella* (*A. catenella*) are enhanced by CO_2, the response is irrespective of nutrient limitations and high temperatures (Tatters et al., 2013). The results, however, from *Karenia brevis* (*K. brevis*) and *Alexandrium minutum* (*A. minutum*) indicated that the modifications of CO_2 levels and temperatures did not have an effect on toxicity (Errera et al., 2014; Flores-Moya et al., 2012). When compared with the results between photosynthesis/growth and toxicity/toxin of HAB, photosynthesis was not only the essential process in primary metabolism but was also required for phycotoxin biosynthesis (Fu et al., 2012; Pan et al., 1996). However, there were inconsistencies in response to climate change because the cells re-allocated the intercellular energy to adapt to the new environment. For example, in *Thalassiosira pseudonana*, the energy metabolism (productions and expenditures) differed in response to environmental changes (e.g., light availability, nitrogen source, and CO_2) (Shi et al., 2015).

As a component of global climate change, elevated atmospheric CO_2 concentrations have led to increased surface temperatures in the ocean, thus influencing water column stratification. The upper mixed layer (UML) has become shallower during warming and freshening events (rain and ice melting). During such events, phytoplankton cells are exposed to higher mean irradiance, e.g., solar PAR and ultraviolet radiation (UVR) (Boyd et al., 2015; Gao et al., 2012a). Most of the previous research, however, has tested the effects of these two factors independently, as reviewed by Fu et al. (2012). Very few studies have focused on the interactive effects of ocean acidification, increased temperature and high irradiance on microalgae (Feng et al., 2008). In particular, the interactive effects on harmful dinoflagellates remain unknown. The HAB species *Akashiwo sanguinea* (*A. sanguinea*) occurs throughout the world (O'Boyle and McDermott, 2014; White et al., 2014; Yang et al., 2012) and frequently forms harmful blooms along the coast of the East China Sea (ECS) in May. The ecologically important features of dinoflagellates blooms which can contribute to the harmful effects are included the productions of shellfish poisons, hemolytic compounds, mucous, etc. The previous reports indicated blooms of *A. sanguinea* had been associated with mass mortalities of invertebrates and fish in various regions of the world (Harper and Guillen, 1989), and negatively effect on seabirds (Jessup et al., 2009). But the toxic mechanism of *A. sanguinea* to marine animals is unclear (Yang et al., 2012). This study was designed to address the interactive effects of OA, warming and high irradiance on *A. sanguinea* by measuring growth rate, photochemical efficiency (F_v/F_m), pigments, ultraviolet-absorbing compounds (UV_{abc}), hemolytic activity and photosynthesis-irradiance curves (P-E curve). The study aims to further elucidate the physiology and toxicity of this species in response to climate change. The present work will deepen the understanding of the effects of multiple factors not only on the physiology but also on the toxicity of this harmful dinoflagellate.

Table 1
Treatment names, experimental growth conditions, and carbonate chemistry for each CO_2 (C, μatm), irradiance (L, μmol photons m^{-2} s^{-1}), and temperature (T, °C) treatment. Mean (±SD, n = 21) values of the parameters of the carbonate system under LC (ambient, 400 μatm CO_2) and HC (enriched, 1000 μatm CO_2) during the experiments. The units of DIC, HCO_3^{1-}, CO_3^{2-} and CO_2 are μmol kg^{-1}. One-way ANOVA (Tukey test) results among the different treatments are indicated by superscript letters. The data with identical superscript letters indicate that the mean values are not significantly different.

Treatments	C	T	L	pH_{NBS}	DIC	HCO_3^{1-}	CO_3^{2-}	CO_2
HCHTHL	1050.0 (50.1)^{a}	28	200	7.82 (0.02)^{c}	2882.5 (202.2)^{ab}	2670.3 (180.9)^{ab}	184.3 (20.7)^{b}	27.97 (0.7)^{b}
HCHTLL	1076.7 (87.4)^{a}	28	50	7.84 (0.01)^{c}	3004.0 (248.0)^{a}	2776.0 (226.9)^{a}	200.2 (19.2)^{b}	27.79 (1.9)^{b}
HCLTHL	1070.0 (26.5)^{a}	20	200	7.74 (0.01)^{d}	2421.3 (165.3)^{b}	2289.9 (155.9)^{b}	97.3 (7.6)^{c}	34.10 (2.2)^{a}
HCLTLL	1076.7 (87.4)^{a}	20	50	7.73 (0.01)^{d}	2302.6 (31.1)^{b}	2178.9 (28.2)^{b}	90.5 (3.3)^{c}	33.21 (0.3)^{a}
LCHTHL	410.0 (36.1)^{b}	28	200	8.16 (0.01)^{a}	2668.6 (234.7)^{ab}	2312.0 (203.3)^{b}	345.5 (30.4)a	11.17 (1.0)^{c}
LCHTLL	403.3 (15.3)^{b}	28	50	8.19 (0.01)^{a}	2838.2 (107.5)^{ab}	2437.0 (92.3)^{ab}	390.2 (14.8)a	10.99 (0.4)^{c}
LCLTHL	403.3 (15.3)^{b}	20	200	8.10 (0.03)^{b}	2286.9 (255.1)^{b}	2072.0 (219.7)^{b}	201.4 (35.0)^{b}	13.53 (0.5)^{c}
LCLTLL	396.7 (15.3)^{b}	20	50	8.09 (0.01)^{b}	2221.2 (56.9)^{b}	2014.8 (51.8)^{b}	193.1 (6.9)^{b}	13.3 (0.5)^{c}