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Dependency of UVR-induced photoinhibition on atomic ratio of N to P in the dinoflagellate *Karenia mikimotoi*

Wanchun Guan[1] · Ping Li[2]

Abstract To investigate the effects of Nitrogen (N):phosphorus (P) ratio and solar ultraviolet radiation (UVR) on the growth and photophosphorylation of oceanic phytoplankton, the effects of UVR and N:P ratio on *K. mikimotoi* were evaluated. *K. mikimotoi* cells were cultured in artificial seawater (ASW) under five different N:P ratios (1:1, 16:1, 50:1, 100:1 and 200:1) for 15 days (phase 1: 1–5 day; phase 2: 6–10 day; phase 3: 11–15 days). Next, *K. mikimotoi* cultures were exposed to photosynthetically active radiation (PAR), PAB (PAR+UV-A+UV-B) and PA (PAR+UV-A), respectively. Finally, *K. mikimotoi* cells grown under the Redfield ratio (16:1) had the largest growth rate (0.257day^{-1}), highest pigment concentrations (chlorophyll a (Chla): 0.465×10^{-5} μg cell^{-1}, carotenoid (Caro): 0.249×10^{-5} μg cell^{-1}) and maximum superoxide dismutase (SOD) activity (0.9 U $\times 10^{-6}$ cell^{-1}) compared with those grown under other N:P ratios. The UV-absorbing compounds' (UV$_{abc}$) absorbance was largest at the N:P ratio of 50:1 during the range of 310–360 nm, with a relatively higher value at the N:P ratio of 16:1. UV intensity was positively correlated with photoinhibition. *K. mikimotoi* cells grown at the N:P ratio of 16:1 showed the smallest photoinhibition compared to those grown at other N:P ratios under the PAR treatment with the largest r:k ratio; similar results were found for both the PA and PAB treatments. The Redfield ratio of 16:1 is optimal for the growth and photophosphorylation of *K. mikimotoi*. The weakest UVR-induced photoinhibition at this ratio may be attributed to the highest photosystem II (PSII) repair rate and SOD activity.

Keywords *Karenia mikimotoi* · Growth rate · N:P ratio · UV radiation · Superoxide dismutase activity · Photoinhibition

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Introduction

Harmful algal blooms are occurring with increasing frequency in recently years around the world, causing serious, unfavorable consequences on ecosystems and public health. *Karenia mikimotoi* (*K. mikimotoi*) is one of the most common harmful algal bloom-forming dinoflagellates, which is widely spread in all of the oceans (Lu and Hodgkiss 2004; Vanhoutte-Brunier et al. 2008).

Ultraviolet (UV) light refers to light with wavelength range of 100–400 nm, generally subdivided into three types, UV-A (315–400 nm), UV-B (280–315 nm) and UV-C (100–280 nm). Solar ultraviolet radiation (UVR) is a natural stress factor for phytoplankton (Beardall and Raven 2004; Häder et al. 2007), and UV-B radiation, in particular, can also change the ultrastructure of chloroplasts (Buma et al. 1996) and affect chlorophyll concentration (Gehrke 1999). UVR can induce rapid decrease in photosystem II (PSII) efficiency, but recovery of photosynthesis is possible if there is sufficient time for repairing of UV damage (Marwood et al. 2000). Furthermore, phytoplankton may acclimate to UV radiation by synthesizing UV-absorbing

compounds (Guan et al. 2011). Moreover, UVR may interact with other environmental factors such as nutrient status (Villafane et al. 2003; Beardall et al. 2009). So far, the interaction between UVR and N:P ratio has never been studied in *K. mikimotoi* yet.

Nitrogen (N) and phosphorus (P) are the primary macronutrients for phytoplankton in the ocean. Although natural phytoplankton normally keeps the N and P at an atomic ratio (N:P) of approximately 16 (Geider and La Roche 2002; Thingstad et al. 2005), the optimal ratio may vary across distinct species (Lagus et al. 2004). High nitrogenous nutrient availability has been suggested to be a prerequisite for *K. mikimotoi* blooms (Chang and Carpenter 1985). The high nutrient concentrations from rivers and human activities are considered to be responsible for the large-scale dinoflagellate blooms that are occurring in the Yangtze River Estuary and adjacent area of the East China Sea from late spring to early summer in the past decade (Anderson et al. 2002; Glibert and Burkholder 2006). The total N concentration in river-diluted water (e.g. the Changjiang River) has been reported to range from 70 to 100 μM, and the most abundant form is NO_3^-–N (Zhiliang et al. 2003; Zhang et al. 2007), while the level of total P is approximately 2–25 μM, with the most common form of particulate P (Yan and Zhang 2003). As a result, the dissolved inorganic N (DIN) to dissolved inorganic P (DIP) ratio (N:P) is typically over 100 at river mouths (Chai et al. 2006; Zhang et al. 2007). However, the N:P ratio is altered because of the P brought from the Taiwan Warm Current (Zhiliang et al. 2003; Fang 2004; Yuan et al. 2008). Thus, the growth of phytoplankton in coastal seawaters commonly fluctuates based on the states of N and P limitation due to discharge from rivers, currents, wastewaters or rainfall.

This study was designed to address the effects of N:P ratio and UVR on *K. mikimotoi* growth and photophosphorylation by measuring growth rate and photochemical efficiency; to further elucidate the molecular mechanisms, concentrations of pigments, UV-absorbing compounds (UV_{abc}) and superoxide dismutase (SOD) were also measured. Our work will deepen our understanding on the effects of N:P ratio and UVR on the growth and photophosphorylation of oceanic phytoplankton.

Materials and methods

Species and culture conditions

K. mikimotoi cells were collected from Dapeng Bay, Guangdong Province, China (22°30′N, 114°20′E) in 2009. *K. mikimotoi* cells were maintained at 20 °C in F/2 medium in a growth chamber (MGC-100P, Shanghai Yiheng Co.

Ltd., China) at 100 μmol photons m^{-2} s^{-1} under cool white fluorescent lights (12L:12D) (Guillard and Ryther 1962). Cells were grown in artificial seawater (ASW) (Berges et al. 2001) with different N:P ratios for three phases (phase 1: 1–5 day; phase 2: 6–10 day; phase 3: 11–15 days), and cell cultures under each N:P ratio were diluted with fresh ASW on days 5 and 10, respectively. After 5–6 generations, the short-term responses of cells to UVR were examined. After 14 days' acclimation, the cultures were diluted to 5×10^3 cells ml^{-1} in fresh ASW medium before exposure to UVR.

Nutrient stoichiometry and treatments

K. mikimotoi cells were grown in ASW medium, with nitrate ($NaNO_3$) and phosphate (Na_2HPO_4) added as the sole sources of N and P, respectively. For each treatment, the phosphate concentration was kept constant at 3.6 μM, while the nitrate concentration was adjusted to between 3.6 and 720 μM to obtain five different N:P ratios (1:1, 16:1, 50:1, 100:1 and 200:1). Cell density was determined in a phyto-chamber by microscopy (CH30RF200, Olympus Optical Co. Ltd., Japan).

UVR radiation treatments

UVR radiation was conducted in an air-conditioned room, where *K. mikimotoi* cells were grown in small (5.9 cm in diameter, 35 cm in length) quartz tubes kept in a water bath containing circulating tap water (20 ± 0.5 °C). To ensure that conditions were comparable during the whole process of the experiments, an artificial UV lamp, a 150-W Xenon lamp (HMI, OSRAM, Germany), was used to provide constant UVR and *K. mikimotoi* cells were grown in artificial seawater containing specific concentration of substrates. The lamp was adjusted to provide 213.3 Wm^{-2} photosynthetically active radiation (PAR), 14.8 Wm^{-2} UV-A, and 6.2 Wm^{-2} UV-B, which were measured by PMA (PMA2100, Solar Light, USA), and the distance from the samples to the front of the lamp was 50 cm. The exposure time was 60 min.

K. mikimotoi cells were exposed to the following treatments: (1) PAB (PAR + UV-A + UV-B), in which tubes were covered with 295 nm cut-off filters (Ultraphan, Digefra, Munich, Germany), transmitting irradiance of above 295 nm; (2) PA (PAR + UV-A), in which tubes were covered with 320 nm cut-off filters (Montagefolie, Folex, Dreieich, Germany), transmitting irradiance of above 320 nm; and (3) PAR, in which tubes were covered with 395 nm cut-off filters (Ultraphan UV Opak, Digefra, Munich, Germany). The filters were provided by Marine Biology Institute, Shantou University. During 60 min of exposure to an artificial UV lamp, photochemical

Fig. 1 Effect of different N:P ratio on the growth, pigment and SOD ▶ activity in *K. mikimotoi*. **a** Cell densities throughout the experiment; **b** the specific growth rates during the three phases ($n = 4$); **c** pigment concentrations (Chla and Caro); **d** SOD activity levels on day 14 as a function of the N:P ratio in the medium, $y = a + bx + cx^2$. The *vertical bars* indicate the SD ($n = 4$), and the *superscripted letters* in **b–d** indicate significant differences among the N:P ratio treatments. There is no significant difference between those with the *same letters*, and there is a significant difference between those with *different letters* ($p < 0.05$). *SOD* maximum superoxide dismutase, *Chla* chlorophyll *a, Caro* carotenoid, *SD* standard deviation, *N:P* nitrogen:phosphorus

efficiency (Y') was measured, and exposure response curves (ERCs) were created.

Measurement of UV$_{abc}$ and pigment concentrations

The spectral characteristics of the cultures were determined by filtering 25–50 ml of *K. mikimotoi* cell cultures (volume varying with cell concentrations) with a Whatman GF/F filter (25 cm in diameter), extraction of pigments in absolute methanol (5 ml) overnight at 4 °C and centrifugation (10 min at 1500 g) (TGL-16GR, Anting, China). Absorbance measurements of the supernatant were obtained from 250 to 750 nm using a scanning spectrophotometer (A590 UV/VIS Spectrophotometer, Xiangyi, China). UV$_{abc}$ concentration was expressed by the peak height (310–360 nm) of optical density. For each treatment, UV$_{abc}$ concentration was measured in triplicate.

Concentrations of chlorophyll a (Chla) and carotenoid (Caro) were calculated using the following equations presented by Porra (Porra 2005) and Strickland & Parsons (Srtickland and Parson 1968), respectively.

$$\text{Chla}(\mu g/ml) = 16.29 \times A_{665.2} - 8.54 \times A_{652}, \tag{1}$$

$$\text{Caro}(\mu g/ml) = 4A_{480}, \tag{2}$$

where $A_{665.2}$, A_{652} and A_{480} are the optical densities (ODs) of the supernatant at 665.2, 652 and 480 nm, respectively. For each treatment, pigment concentration was measured in triplicate.

Measurement of *K. mikimotoi* growth rate

Samples were taken daily for cell counting, and specific growth rate (μ) was calculated as follows:

$$\mu = \ln \left(C_n/C_{n-1} \right)/\left(t_n - t_{n-1} \right), \tag{3}$$

where C_n and C_{n-1} are the cell concentrations (cells ml^{-1}) over the ($t_n - t_{n-1}$) period. For each treatment, growth rate was measured in triplicate.
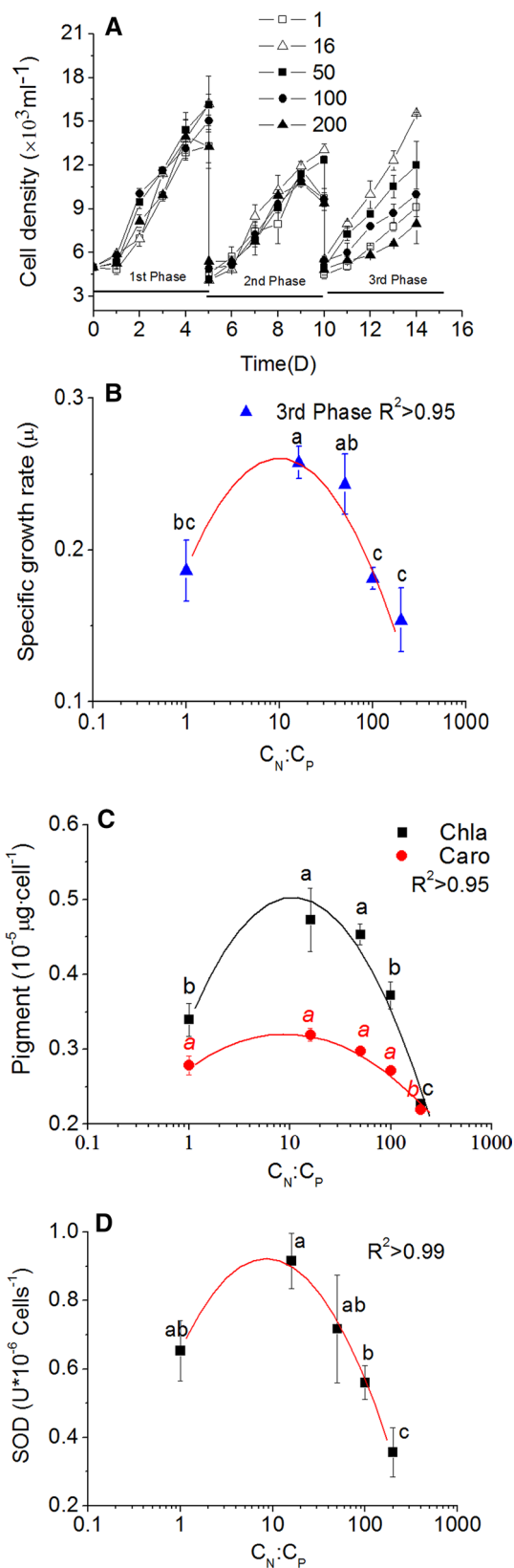
Measurement of photochemical efficiency, repair rate (r) and damage rate (k)

K. mikimotoi cultures were exposed to PAR, UV-A + PAR and UVR (PAR + UV-A + UV-B) for 60 min. Photochemical efficiency was measured every 5–30 min during the exposure period. Effective photochemical efficiency (Y') was measured with a PSI fluorometer (AquaPen-C, Photon System Instruments, Czech Republic) and calculated according to Genty et al. (Genty et al. 1990) as follows:

$$Y' = \Delta F/F_m' = \left(F_m' - F_t\right)/F_m', \tag{4}$$

where Y' was determined by measuring the instant maximal fluorescence (F_m') and the steady-state fluorescence (F_t) of light-adapted cells. The saturating light pulse was 3000 µmol photons m^{-2} s^{-1}, with a duration time of 0.6 s. The light intensity at the time of measurement was approximately 0.3 µmol photons m^{-2} s^{-1}, and actinic irradiance was 10 µmol photons m^{-2} s^{-1}.

The rate of UVR-induced damage to the photosynthetic apparatus (k, in min^{-1}) and corresponding repair rate (r, in min^{-1}) were estimated according to previous studies (Beauchamp and Fridovich 1971; Lesser et al. 1994) as follows:

$$Y_n'/Y_0' = r/(r+k) + k/(k+r) * e^{-(k+r)t}, \tag{5}$$

where Y_n' and Y_0' are Y' values at time t_n or t_0, respectively.

UVR-induced inhibition of effective photochemical efficiency was calculated as follows:

$$\text{Inh}(\%) = \left(Y_P' - Y_x'\right) \times Y_P^{-1} \times 100, \tag{6}$$

where Y_P' is Y' under PAR treatment, and Y_x' is Y' under PA or PAB treatment.

Artificial UV light-induced inhibition (i.e. PAR, PA and PAB) was calculated as follows:

$$\text{Inhibition}(\%) = \left(Y_0 - Y_{60}\right) \times Y_0^{-1} \times 100,$$

where Y_0 indicates the initial value (control), and Y_{60} is Y' after 60 min of exposure to the PAR, PA or PAB.

Extraction and measurement of superoxide dismutase (SOD)

First, SOD was extracted as follows: 100 ml of *K. mikimotoi* cell cultures (cell density of approximately 5000 cells ml^{-1}) were harvested by centrifugation at 2500g for 5 min, and the resulting pellet was resuspended in 3 ml phosphate-buffered saline (PBS) (pH 7.5). The mixture was then sonicated 20 times as follows: 3 pulses with 20 s intervals at a fixed amplitude of 20 µm (JY92-IIN, Ultrasonic Processor, Xinzhi Inc., China). The supernatant was collected after centrifugation at 10,000g for 15 min at 4 °C (TGL-16GR Benchtop High-Speed Refrigerated

Centrifuge, Anting, China). Next, reaction reagents were added following the manufacturer's protocol (Keming Biotechnology Ltd. Com., Suzhou, China) to measure SOD activity. SOD activity was determined by measuring the inhibition of photochemical reduction of nitroblue tetrazolium (NBT) at 560 nm (A590 UV/VIS spectrophotometer, Xiangyi, China), as suggested by Beauchamp and Fridovich (Heraud and Beardall 2000). One unit of SOD (per cell) was defined as the amount causing 50% inhibition of the photochemical reduction of NBT. Each treatment was performed in triplicate.

Data analysis

Growth rate, SOD, UV$_{abc}$ and pigment concentration were expressed as mean ± standard deviation (SD). Each radiation treatment was performed in quadruplicate, and for each determination of the effective photochemical efficiency, at least two measurements were performed; thus,
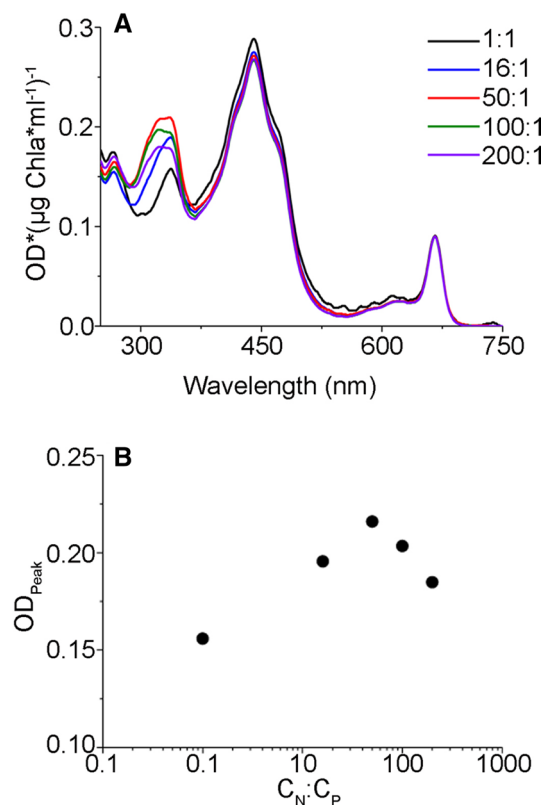

Fig. 2 Effect of different N:P ratio on UV$_{abc}$. **a** Spectral absorption characteristics of *K. mikimotoi* (methanol extraction) at the end (t$_{14}$) of culture acclimation to five different N:P ratios, respectively; The *lines of black, blue, red, green* and *purple colors* represent the N:P ratios of 1:1, 16:1, 50:1, 100:1 and 200:1, respectively. **b** The peak (310–360 nm) in optical density (OD$_{Peak}$) after the 14-day acclimation period. *N:P* nitrogen:phosphorus, *UV* ultraviolet, *OD* optical density, *Chla* chlorophyll *a*

Fig. 3 Changes in effective photochemical efficiency (Y') in *K. miki-* ▶
motoi during 60 min of exposure to PAR, PA and PAB under a UV
lamp. The *letters* **a–e** indicate the following N:P ratios in the media: **a**
1:1; **b** 16:1; **c** 50:1; **d** 100:1; **e** 200:1. The *vertical bars* represent the
SD ($n = 8$). *PAR* photosynthetically active radiation, *PA* PAR + UV-A,
PAB PAR + UV-A + UV-B, *UV* ultraviolet, *N:P* nitrogen:phosphorus,
SD standard deviation

a total of eight measurements were used to calculate the
mean and SD. One-way analysis of variance (ANOVA)
was used to determine whether there was a significant
difference among different treatments with $P < 0.05$ as
cutoff (Larson 2008). All statistical analyses were per-
formed using SPSS V20.0 (SPSS, Inc., Chicago, USA).

Results

Effects of N:P ratio on growth rate, pigment and UV$_{abc}$ concentrations and SOD activity

In the first two phases of acclimation, the growth rates
under five different N:P ratio conditions were similar,
regardless of the external N:P ratio in the media (Fig. 1a).
In the third phase, *K. mikimotoi* cells grown at the N:P
ratio of 16:1 exhibited the largest growth rate (0.257
day^{-1}), while those grown under a higher or lower N:P
ratio inhibited lower growth rate ($P < 0.05$) (Fig. 1a).
Association between growth rate and N:P ratio during
the third phase was fitted using the two-order equation $y
= a + b \times x + c \times x^2$ ($R^2 > 0.95$) (Fig. 1b), and the growth
rate of cells under the N:P ratio of 16:1 was significantly
higher than that under any other ratio except the ratio of
50:1 ($P < 0.05$).

The concentration of pigment (both chla and caro)
also peaked (chla: 0.465×10^{-5} µg cell^{-1} and caro:
0.249×10^{-5} µg cell^{-1}) at the N:P ratio of 16:1, while
the lowest concentration was observed at 200:1 (chla:
0.227×10^{-5} µg cell^{-1} and caro: 0.124×10^{-5} µg cell^{-1})
(Fig. 1c). And there was a strong positive correlation
between pigment and N:P ratio ($R^2 > 0.95$).

Antioxidant (SOD) activity also had the highest level
($0.9 \text{ U} \times 10^{-6}$ cells^{-1}) at the N:P ratio of 16:1 (Fig. 1d),
and a two-order equation was fitted $y = a + b \times x + c \times x^2$
($R^2 > 0.99$).

The UVabc absorbance was largest at the N:P ratio of
50:1 during the range of 310–360 nm, while it was the
smallest at the N:P ratio of 1:1, and it was also relatively
higher at the N:P ratio of 16:1 (Fig. 2a), indicating a rel-
atively higher UVabc concentration. And there were no
significant correlations between absorbance and N:P ratio
(Fig. 2b).
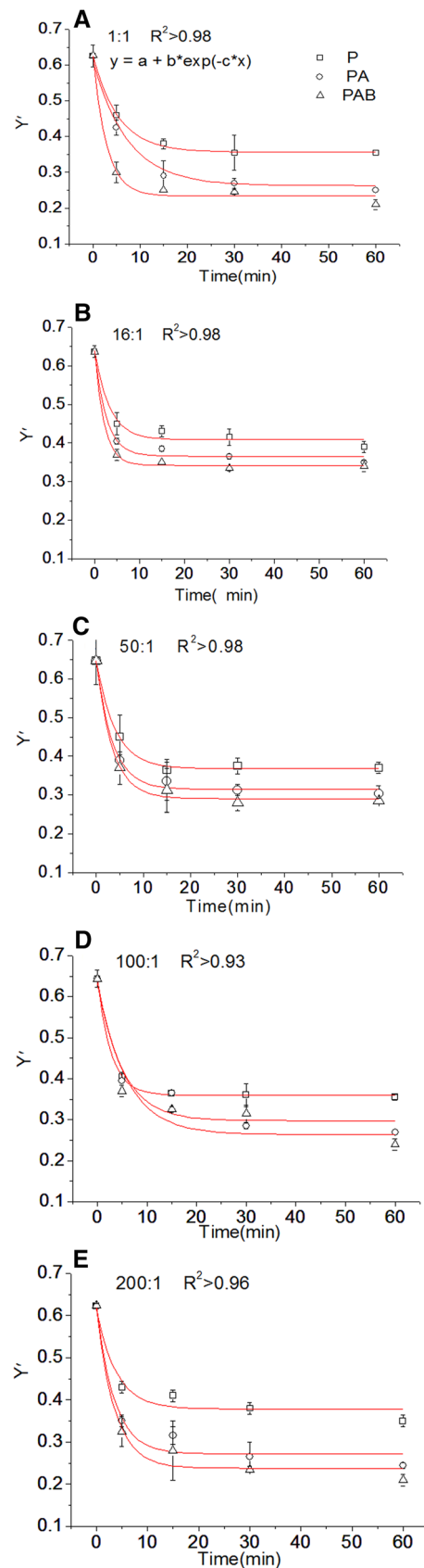
Effects of N:P ratio and radiation intensity on photochemical efficiency

The effective photochemical efficiency (Y') data were fitted using a first-order exponential equation ($y = a + b \times \exp(c \times t)$) (Fig. 3). *K. mikimotoi* cells exposed to PAR + UV-A + UV-B showed largest decrease at each N:P ratio (1:1, 16:1, 50:1, 100:1 and 200:1), and those
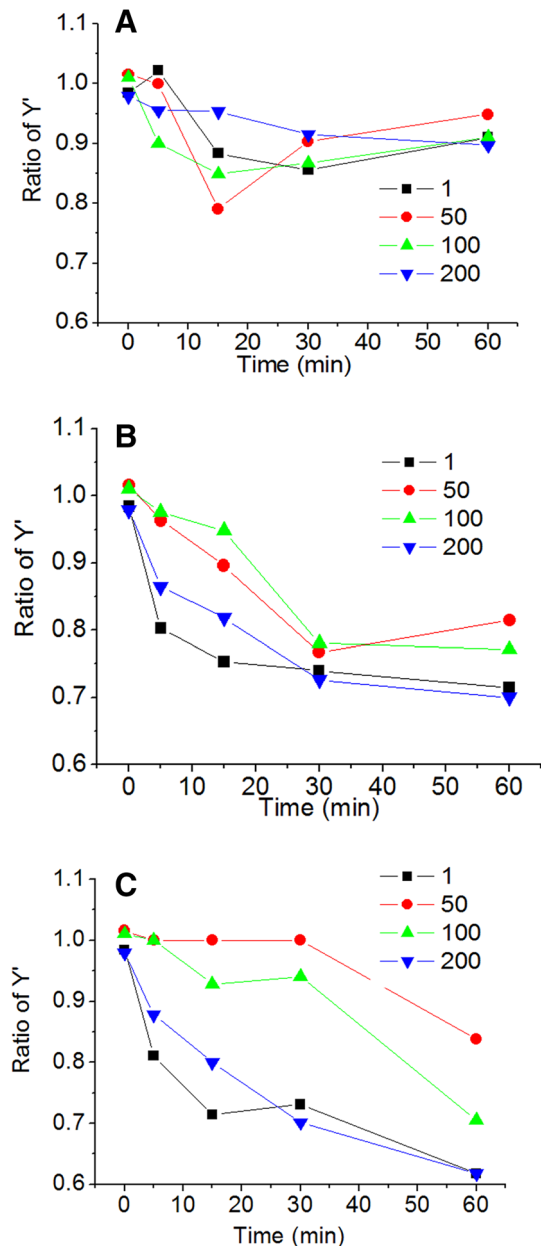
exposed to PAR showed the smallest decrease, indicating that the damage of the PSII was associated with the degree of radiation. Meanwhile, *K. mikimotoi* cells grown at the N:P ratio of 16:1 showed the samllest decrease in effective photochemical efficiency compared to those grown at other N:P ratios (1:1, 50:1, 100:1 and 200:1), with the ratio of Y' value at other N:P ratios to that at 16:1 beling samller than 1 at most time points (Fig. 4), indicating that the N:P ratio of 16:1 can alleviate the unfavaroble effects UVR on *K. mikimotoi* photophosphorylation.

Determination of repair and damage rate and UVR-induced photoinhibition

The rate of UVR-induced damage to the photosynthetic apparatus (k, in min^{-1}) and corresponding repair rate (r, in min^{-1}) were estimated according to the ERCs above. Repair rate was more sensitive to the N:P ratio compared with the damage rate, as the latter seemed to show no change at different N:P ratios under each radiation treatment (Fig. 5a, b). Furthermore, *K. mikimotoi* exposed to PAR had the largest repair rate (Fig. 5a); so did the r/k ratio (Fig. 5c). The smallest Y_{60}'/Y_0' value (38.74%) was observed at the N:P ratio of 16:1 in *K. mikimotoi* exposed to PAR, indicating the weakest photoinhibition at this ratio; similar results were observed for those subject to PA and PAB treatments; furthermore, *K. mikimotoi* exposed to PAR had the smallest Y_{60}'/Y_0' value compared to those suject to PA and PAB treatments at the same N:P ratio (Fig. 5d). Finally, it was found there was an obvious negative linear correlation between r:k and photoinhibition (Fig. 5e). Meanwhile, there was a close positive correlation between UVR-induced photoinhibition and N:P ratio (Fig. 6a) and a negative correlation between UVR-induced photoinhibition and SOD activity (Fig. 6b).

Fig. 4 The effective photochemical efficiency (Y') ratio of X to Y' at 16:1 (N:P). *X-axis* indicates the ratio of Y' at 1:1, 50:1, 100:1 and 200:1, respectively. **a** The Y' ratio for the PAR treatment; **b** the Y' ratio for the PA treatment; and **c** the Y' ratio for the PAB treatment. *N:P* nitrogen:phosphorus, *PAR* photosynthetically active radiation, *PA* PAR + UV-A, *PAB* PAR + UV-A + UV-B

Discussion

Effects of N:P ratio on *K. mikimotoi* growth

N is an indispensible component of Chla and proteins involved in (Geider et al. 1993) (Geider et al. 1998); P level affects ATP/ADP ratio; thus P limitation impacts the Kelvin cycle (Brooks 1986). In the present study, the effects of intracellular N and P pools disappeared after 10 days' acclimation, and the growth of *K. mikimotoi* was observed to be significantly influenced by the environmental N:P ratio during the third period. Redfield (Redfield 1958) has reported that the C:N:P ratio in normal seawater is 106:16:1 (Redfield ratio), that is, the optimum N:P ratio is approximately 16:1, and other ratios, such as N:P>22 or <10, have been proposed to cause P and N limitation,

Fig. 5 The repair rate, damage rate, *r:k* ratio under the PAR, PA ▶ and PAB treatments as a function of the N:P ratio in the medium. **a** The repair rate (*r*, min^{-1}); **b** damage rate (*k*, min^{-1}); **c** the *r:k* ratio; **d** the Y_{60}' to Y_0' ratio as a function of the *r:k* ratio. **e** the *r:k* ratio as a function of the Y_{60}' to Y_0' ratio. The *vertical* and *horizontal* bars represent the SD (*n* = 8). *PAR* photosynthetically active radiation, *PA* PAR + UV-A; PAB, PAR + UV-A + UV-B, *N:P* nitrogen:phosphorus, *SD* standard deviation

respectively (Justić et al. 1995). Nutrient limitation hinders the growth of microalgae, and levels of pigments, proteins, and enzymes in microalgae (Geider et al. 1993, 1998; John and Flynn 2000; Lippemeier et al. 2001). This agrees with our finding that *K. mikimotoi* cells grown at the N:P ratio of 16:1 exhibited the largest growth rate. Actually, many previous studies have confirmed the unfavorable effects of P and N limitation on the growth of phytoplankton, such as *Dunaliella salina* (Lippemeier et al. 2001), *Alexandrium fundyense* (John and Flynn 2000), *Scenedesmus* sp. (Rhee 1978), and *Chlamydomonas reinhardtii* (Weers and Gulati 1997).

The highest Chla, Caro and UV_{abc} concentrations at the N:P ratio of 16:1 may contribute to the largest *K. mikimotoi* growth rate detected here. N is the raw material for the synthesis of both UV_{abc} and Chla (Geider et al. 1993). Furthermore, N or P limitation seems to have more significant effect on Chla than on Caro and UV_{abc}.

The dependence of UVR-induced photoinhibition on N:P ratio on *K. mikimotoi*

Previously, Shelly et al. have reported that UV radiation can significanetly accelerate the decline in growth rate and fluorescence parameters caused by P starvation (Shelly et al. 2005), suggesting the interaction between UVR and nutrient condition. Here, we found UVR-induced photoinhibition was associated with the degree of radiation at each N:P ratio. Meanwhile, UVR caused the weakest inhibition of effective photochemical efficiency at the Redfield ratio, suggesting that the Redfield ratio (N:P ratio of 16) can alleviate the unfavoroble effects of UVR on photophosphorylation. This may be attributed to that the PSII repair rate, SOD activity and pigment concentraitons were the highest at this ratio.

Photoinhibition has been attributed to the imbalance between the rate of photodamage to PSII and the rate of the repair of damaged PSII (Murata et al. 2007). Thus, the higher repair rate observed at the Redfield ratio is conducive to the alleviation of UV-induced inhibition. Meanwhile, higher SOD activity also helps to weaken UVR-induced photoinhibition, and many studies have confirmed that SOD can prevent UVR-induced oxidative stress (Zu et al. 2011) (Wang et al. 2008).
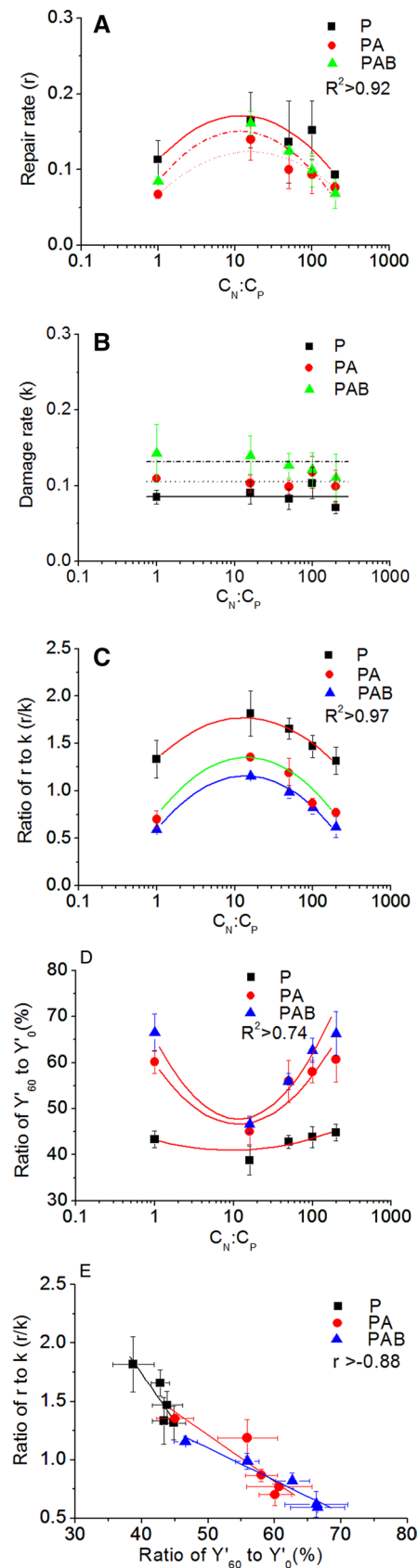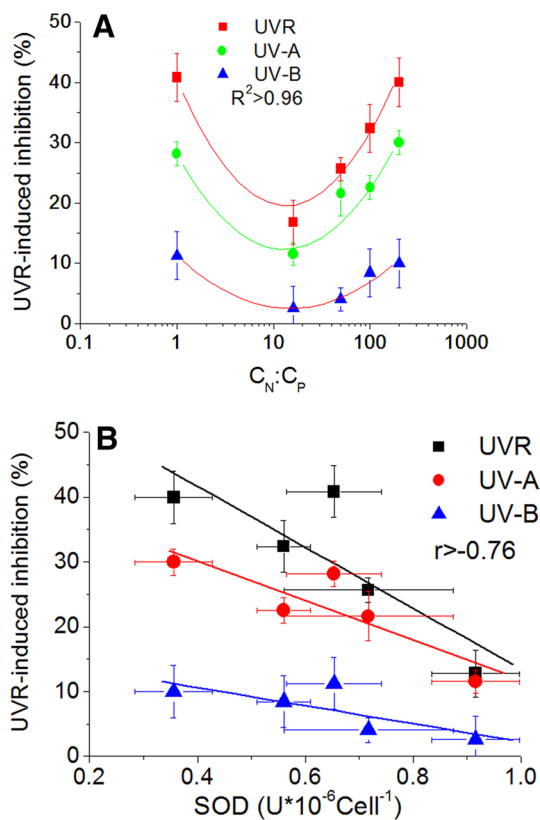
Fig. 6 Associations between UVR-induced photoinhibition and N:P ratio, as well as SOD activity. **a** UVR-induced photoinhibition as a function of the N:P ratio in the medium; **b** UVR-induced photoinhibition as a function of the SOD activity in *K. mikimotoi*. The *vertical* and *horizontal bars* represent the SD ($n = 4$–8). *UVR* ultraviolet radiation, *N:P* nitrogen: phosphorus, *SOD* maximum superoxide dismutase, *SD* standard deviation

Accumulation of UV_{abc}, such as mycosporine-like amino acids, has been recognized as a self-protection mechanism in phytoplankton and acclimation strategy in response to UV, especially UV-B stress (Sinha and Häder 2008). However, the effects of N:P ratio on UV_{abc} concentration has never been reported, and no significant differences were found in UV_{abc} concentration between *K. mikimotoi* cells grown under different N:P ratios in the present study.

In conclusion, the Redfield ratio of 16:1 is optimal for the growth and photophosphorylation of *K. mikimotoi*. The weakest UVR-induced photoinhibition at this ratio may be attributed to the highest PSII repair rate and SOD activity. Our work has presented the interaction between N:P ratio and UVR on *K. mikimotoi* growth and photophosphorylation for the first time.

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