

**Effect of aerosol
input on
phytoplankton
community structure**

C. Guo et al.

**Dynamics of phytoplankton community
structure in the South China Sea in
response to the East Asian aerosol input**

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Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Abstract

Recent studies have regarded atmospheric deposition as an increasingly important source of nutrients to the ocean. The South China Sea (SCS), where aerosol loading is among the highest in the world, however, is poorly studied particularly on the in situ changes of phytoplankton community structures in response to atmospheric deposition. By conducting a series of microcosm bioassays at different hydrographical locations and simulating different aerosol event scales, we observed both positive and negative responses induced by the input of East Asia (EA) aerosol with high nitrogen (N) and trace metal contents, in terms of both community structure and physiological characteristics of phytoplankton. High levels of aerosol loading profoundly relieved phytoplankton nitrogen and trace metal limitations in SCS, and thus increased total phytoplankton biomass, enhanced their physiological indicators (e.g. photosynthetic efficiency) and shifted phytoplankton assemblages from being dominated by picoplankton to microphytoplankton, especially diatoms. However, under low levels of aerosol loading, the composition shift and biomass accumulation were not apparent, suggesting that the stimulation effects might be counterbalanced by enhanced grazing mortality indicated by increased abundance of protist grazers. Trace metal toxicity of the aerosols was also an important negative factor to phytoplankton growth, especially picocyanobacteria, implicated by the high copper (Cu) concentration in the microcosm that surpassed the toxicity threshold of marine cyanobacteria. Moreover, the magnitude and duration of the deposition event, as well as the hydrographical and trophic conditions of receiving waters are also important factors when predicting the influence of an aerosol deposition event. Our results demonstrated that the EA aerosol deposition events could profoundly change nutrient and phytoplankton dynamics in SCS and highlighted the need for achieving an accurate comprehension of atmospheric nutrient on the biogeochemical cycles of the oceans.

Effect of aerosol input on phytoplankton community structure

C. Guo et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



1 Introduction

Human activities have profoundly fuelled the generation of industrial and agricultural emissions in the last few decades (Akimoto et al., 2003). These anthropogenic sources, as well as natural sources (e.g. desert and volcano dust), in the form of gases and particles, can be returned to the land and sea via diverse atmospheric depositional processes (Zheng et al., 2005). For example, the biologically active entities may be delivered constantly throughout the year by dry deposition; in a pulse driven by an episodic release; or periodically due to environmental fluctuations. Recent studies have regarded atmospheric aerosol deposition as an increasingly important source of nutrients (mainly macronutrients and trace metals) to the ocean, altering the patterns of the Earth's biogeochemistry (Jickell et al., 2005; Duce et al., 2008). As much as 450 Tg of dust reach the oceans per year, accounting for 26 % of total dust flux produced. An estimated flux of 67 Tg reactive N, which accounts for up to one third of the ocean's external N supply, and 16 Tg iron (Fe), which is the dominant source of Fe for the surface waters of open oceans, are contained in the dust depositions, with possible implications on biological productivity (Duce et al., 1991, 2008; Jickell et al., 2005).

Aerosol input to the oceans' surface is an important forcing influencing the phytoplankton community structure, growth rate, primary production, and new production (Paerl, 1997; Duce et al., 2008). Atmospheric Fe input can relieve the Fe limitation on primary production occurring in about 30 % of the oceans, especially in the "high-nitrate low-chlorophyll" (HNLC) regions (Martin et al., 1989; Falkowski et al., 1998). A study in the Northeast Atlantic suggested that aeolian deposition of Fe could result in a 17 % increase of primary production in the region (Brust and Waniek, 2010). The relief of Fe stress by atmospheric supply can change phytoplankton species composition by species-selective relief of Fe stress and stimulate N fixation (Jickells et al., 2005). In addition to macronutrients and Fe, the atmospheric supply of other trace metals, such as copper (Cu), zinc (Zn), lead (Pb) and cadmium (Cd), to the ocean is also significant (Duce et al., 1991; Paytan et al., 2009). These aerosol-derived trace metals can be

BGD

8, 6637–6680, 2011

Effect of aerosol input on phytoplankton community structure

C. Guo et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Effect of aerosol input on phytoplankton community structure

C. Guo et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



highly enriched and transported in biogenic particles in oceanic surface waters, which has been suggested to be an important mechanism for trace metal cycling in global oceans (Ho et al., 2010). Marine biogeochemical cycling and the carbon budget have been reported to be sensitive to variations in atmospheric nutrient deposition (Martin, 1990; Doney et al., 2007; Krishnamurthy et al., 2007). Atmospheric deposition has also been suggested to shift the nitrogen/phosphorus (N/P) stoichiometry in oligotrophic oceans (Falkowski, 1997) and lakes (Elser et al., 2009), due to the high N/P ratio in those aerosols (Baker et al., 2003; Paytan et al., 2009).

The northwest Pacific region, especially the Chinese marginal seas, which are located downwind of East Asia (EA) with large human population densities and high levels of industrial and agricultural activities, receives increasingly high aerosol deposition originating from the Gobi desert and is mixed with industrial and agriculture emissions, as well as anthropogenic biomass burning (Duce et al., 1991; Lin et al., 2007; Uematsu et al., 2010). The input of N, Fe and other trace metals, through the atmospheric deposition of dust, is among the highest to oligotrophic waters in the world (Duce and Tindale, 1991; Paytan et al., 2009). It has been reported that the atmospheric deposition of dust to the Chinese marginal seas is 67 Tg yr^{-1} , accounting for 14 % of the total atmospheric dust deposition to the entire North Pacific (Gao et al., 1997). As such, this region has become another high-atmospheric-deposition region along with the Mediterranean and North Atlantic that are exposed to Sahara dust (Prodi and Fea, 1979; Ridame and Guieu, 2002; Prospero and Lamb, 2003), thus attracting researchers' attention in recent years (Gao et al., 1997; Uematsu et al., 2010). Different from the composition of European and North American aerosol, the Asian aerosol is likely to be a more complex mixture which not only contains significant amounts of natural mineral dust, but also a substantial portion of anthropogenic polluted aerosols with high concentrations of N, Fe and other trace metals, such as combustion-derived ionic, organic and soot particles (Chameides et al., 1999; Cohen et al., 2004; Paytan et al., 2009). These anthropogenic aerosols have a relatively small size, which permits them to have a long life, i.e. from hours to weeks, being transported for long distances

in the range of thousands of kilometers to the South China Sea (SCS), especially in winter when the northeast monsoon prevails (Chameides et al., 1999). Therefore, the unique characteristics and the increasing of the EA aerosol input create an urgency to understand their impact on the northwest Pacific marine ecosystem.

SCS is one of the largest marginal seas in the world, located in the subtropical and tropical northwest Pacific Ocean. The seawater is oligotrophic, especially in the central basin. The concentrations of N and P in the euphotic layer are usually below detection limits using conventional methods, and concentrations of chlorophyll (Chl) *a* are also low (Gong et al., 1999). Picoplankton dominate the phytoplankton assemblages (Liu et al., 2007). Therefore, in this “high aerosol, low Chl” region, the effects of atmospheric aerosol loading on phytoplankton community structures and biogeochemistry were suggested to be significant (Wong et al., 2002; Wu et al., 2003; Lin et al., 2007).

Some enrichment bioassay experiments conducted in the Mediterranean and North Atlantic Ocean using the Sahara dust have supported the hypothesis that aeolian dust deposition can stimulate N fixation, phytoplankton growth and enhance primary production by supplying both P and Fe (Ridame and Guieu, 2002; Guieu et al., 2002; Mills et al., 2004). In the Northwest Pacific, several assessments based on modeling and remote sensing data have suggested that the aerosol loadings have a tight connection with increased biological production and coastal eutrophication (Lin et al., 2009; Onitsuka et al., 2009, Sundarambal et al., 2010). Paytan et al. (2009) used a model to predict the aerosol toxicity to the SCS region based on theoretical deposition fluxes and toxicity thresholds. However, there is a lack of field data to prove the toxicity effect predicted by modeling and to reveal the in situ response of the autotrophic assemblages in this region to the input of EA aerosol. With the goal of understanding the effects of EA aerosol deposition on phytoplankton community structure and production in SCS, a series of atmospheric aerosol enrichment bioassays using EA aerosol samples and SCS surface seawater were performed to elucidate the following 2 questions: (1) how do EA aerosols affect the phytoplankton in terms of both species composition and physiological characters? (2) Will some environmental fluctuations, such as the magnitude and

BGD

8, 6637–6680, 2011

Effect of aerosol input on phytoplankton community structure

C. Guo et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



duration of the deposition event, and the hydrographic and tropic conditions of receiving water influence the impact? To our knowledge, this is the first report describing the interaction between EA aerosol deposition and phytoplankton community dynamics in the Northwest Pacific region.

2 Methods

2.1 Atmospheric aerosol collection and treatment

Aerosol samples were collected locally on the rooftop of the Academic Building at the Hong Kong University of Science and Technology (HKUST). HKUST is located at the eastern side of Hong Kong adjacent to the Port Shelter and SCS. The university is in a relatively low populated area and the nearest commercial area is more than 5 km away. The sampling was conducted on a sunny day in December 2010 when the northeast monsoon prevailed. Aerosol particles smaller than $2.5\ \mu\text{m}$ in aerodynamic diameter were collected onto 8×10 -inch Quartz filters (#2500 QAT-UP, Pall Life Science, Ann Arbor MI, USA) using a high-volume sampler operated at a flow rate of $1130\ \text{l min}^{-1}$ for 24 h. The weight of aerosol on the filter was about 70 mg, which was a very rough value estimated using in situ PM 2.5 concentration data obtained from the Environmental Central Facility (ENVF/ IENV) Atmospheric & Environmental Database of HKUST. The sampling height was about 100 m above sea level. After sample collection, the filters were stored at -20°C . Before the cruise, the aerosol filter was dissolved in 450 ml pre-filtered seawater (by $0.02\ \mu\text{m}$ PC membrane), followed by $0.2\ \mu\text{m}$ filtration, to make the aerosol leachate.

2.2 Study area, seawater collection and experimental design

The experiments were conducted during November 2009 to January 2010 in Port Shelter, a bay on the east coast of Hong Kong, and during the “Carbon Cycling in China

BGD

8, 6637–6680, 2011

Effect of aerosol input on phytoplankton community structure

C. Guo et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Effect of aerosol input on phytoplankton community structure

C. Guo et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Seas-budget, controls and ocean acidification” (CHOICE-C) cruise in SCS (Fig. 1). Surface seawater was collected and the aliquot (4L) was incubated in acid-cleaned bottles after 200 μm pre-screening to exclude mesozooplankton. They were immediately amended with aerosols or inorganic nutrients as described in Table 1. The incubations were conducted in an on-deck incubator with temperature controlled by running seawater and covered by two layers of neutral density screen to attenuate the sunlight intensity by $\sim 40\%$. The bottles were gently stirred twice a day. All experimental treatments were performed in triplicate. The incubation bottles and laboratory wares were soaked in 10% HCl, thoroughly washed with Milli-Q water and rinsed with experimental seawater prior to use.

Five on-board microcosm experiments which can be grouped into three kinds of enrichment bioassays (Table 1) were performed at 5 stations (Fig. 1) to monitor the responses of the phytoplankton community structure to atmospheric aerosol deposition. In the microcosm Experiment 1, pre-leached atmospheric aerosol was initially enriched in seawater samples with zero (control), low and high concentrations (Table 1) to simulate the episodic atmospheric conditions (e.g. dust storm, typhoon, and heavy rainfall). In the Experiment 2, the aerosol leachate was amended daily with control, low and high aerosol concentrations, using oceanic seawater at station S412, to mimic continuous atmospheric deposition. Experiment 3 was designed to assess the key nutrients in the aerosol that affects phytoplankton growth in SCS. Aerosols as well as inorganic nutrients were added in the seawater collected at station A1 (Table 1).

2.3 Subsampling and parameter measurement

Samples for measurements of picoplankton, heterotrophic protists, and maximum photochemical efficiency of photosystem II (PSII) (Fv/Fm) were taken every 24 h after nutrient amendments. Other subsamples were removed at the start and end of incubation for analysis of the following parameters: dissolved inorganic nutrients, Chl a, microplankton (phytoplankton between 20–200 μm), and photosynthetic pigments.

2.3.1 Chl *a*

Duplicate aliquots of 200–1000 ml subsamples were sequentially filtered through 20 µm polycarbonate membranes and Whatman GF/F glass fiber filters, which were then extracted with 90 % acetone at –20°C in the dark overnight and determined fluorometrically using a Turner Designs Trilogy fluorometer (Strickland and Parsons, 1972).

2.3.2 Fv/Fm

The maximum photochemical efficiency of PSII (Fv/Fm) was determined by a Fluorescence Induction and Relaxation (FIRe) System (Satlantic Inc.). Samples were dark adapted for 30 min at in situ temperatures before measurement. Data collection and processing were conducted following the manufacturer's protocols.

2.3.3 Inorganic nutrients

Samples for measurement of inorganic nutrients in the aerosol seawater leachate (nitrate, nitrite, ammonium, phosphate and silicate) were filtered through GF/F glass fiber filters, and the filtrates immediately frozen at –20°C until analysis. The concentrations of inorganic nutrients were determined colorimetrically using a Skalar autoanalyzer (San Plus) following JGOFS protocols (Knap et al., 1996). The data of in situ inorganic nutrient concentrations at each station (Table 1) were provided by Dai, M.

2.3.4 Trace metal measurements

The trace metal concentrations in the aerosol leaching solution were determined. The leachate samples were diluted 100- to 1000-fold with 3% super-pure nitric acid (Seastar) with Element grade Milli-Q water in a class 100 trace-metal clean bench, which were ready for inductively coupled plasma mass spectrometer (ICPMS) analysis. The concentrations of all trace metals analyzed were determined by using a sector field double-focusing high-resolution ICPMS (Element XR, Thermo Scientific), fitted

Effect of aerosol input on phytoplankton community structure

C. Guo et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



with a de-solvation system (APEX and Spiro, Elemental Scientific Inc.). The sensitivity and stability of the instrument was adjusted to optimal condition before analysis. The analysis was conducted with sensitivity above 10^6 counts per second for 1 ppb indium standard and the analytical precision was normally between 1 % and 2 %. External and internal standards were both applied for concentration quantification. The details of the analytical accuracy and detection limits of the ICPMS method are described in Ho et al. (2007).

2.3.5 Microphytoplankton and ciliate identification

100 ml subsamples for enumeration of microplankton were fixed with acidic Lugol's solution (final concentration 5 %) and stored in amber plastic bottles at room temperature for microscopic observation. Samples of 10–30 ml were concentrated by settling for 24 h in glass cylinders. Microplankton were identified and counted under an Olympus IX51 inverted microscope.

2.3.6 Picoplankton and heterotrophic nanoflagellate (HNF) enumeration

Autotrophic picoplankton and HNF were enumerated using a Becton-Dickson FAC-SCalibur Flow Cytometer under high flow rate of $60 \mu\text{l min}^{-1}$. Samples (1.8 ml) were fixed with 0.5 % seawater buffered paraformaldehyde and stored at -80° before analysis. Abundances of picoplankton (*Prochlorococcus*, *Synechococcus*, and picoeukaryotes) were discriminated according to the side scattering (SSC) and red/orange auto-fluorescences emitted by chlorophyll/phycoerythrin (Olson et al., 1993). For counting the heterotrophic nanoflagellate (HNF), the samples were stained with 0.01 % SYBR Green-I (Invitrogen) and then incubated under 37°C for 40 min. The method for HNF enumeration was according to Zubkov et al. (2007). Yellowish green fluorescence beads ($1 \mu\text{m}$, Polysciences) were added as an internal standard. Flow cytometric data were analyzed using WinMDI software 2.9 (Joseph Trotter, Scripps Research Institute, La

BGD

8, 6637–6680, 2011

Effect of aerosol input on phytoplankton community structure

C. Guo et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Jolla, CA, USA). The values of SSC signal and red fluorescence emission were normalized to beads, and used as the proxy of cell size and cellular chlorophyll.

2.3.7 Pigment analysis by high-performance liquid chromatography (HPLC)

Seawater samples (1.9–6 l) for pigment analysis were filtered onto 25 mm Whatman GF/F filters under a gentle vacuum (<0.2 MPa). Filters were wrapped in aluminum foil and stored at -80°C . The pigment concentrations were detected using High Performance Liquid Chromatography (HPLC) following the modified method of Furuya et al. (1998). The filter was soaked in 2 ml *N,N*-dimethylformamide (DMF) extraction at -20°C for 2 h. The extraction was then filtered through 13 mm Whatman GF/F filters (Swinnex Filter Holder) to clean the debris and mixed with 1 mol l^{-1} ammonium acetate (600 μl :600 μl). Each mixture was partially injected into an Agilent series 1100 HPLC system fitted with a $3.5\text{ }\mu\text{m}$ Eclipse XDB C_8 column ($100 \times 4.6\text{ mm}$; Agilent Technologies). Quantification was confirmed by the standards that were purchased from Danish Hydraulic Institute [DHI] Water and Environment, Hørsholm, Denmark.

2.3.8 Statistical analyses

One-way ANOVA was conducted to assess if the differences in selected parameters were significant among different treatments and controls using SPSS.

3 Results

3.1 Characteristics of surface seawaters and aerosol samples

The sampled seawater used for experiments was oligotrophic as indicated by low Chl *a* and macronutrient concentrations (Table 2). Concentrations of inorganic N were below $1\text{ }\mu\text{mol l}^{-1}$, decreasing from the coastal station PM7, to shelf stations C3a and A1, and to oceanic stations SEATs and S412. Initial P concentrations were below the

BGD

8, 6637–6680, 2011

Effect of aerosol input on phytoplankton community structure

C. Guo et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



detection limit ($0.08 \mu\text{mol l}^{-1}$) at all the stations except PM7. Low Chl *a* concentrations ($<0.5 \mu\text{g l}^{-1}$) were observed, with a declining trend along the onshore-offshore gradient. Generally, pico- ($0.2\text{--}2 \mu\text{m}$) and nano-sized ($2\text{--}20 \mu\text{m}$) phytoplankton dominated in total Chl *a* at all stations (64%–92%). The contribution of micro-sized cells ($>20 \mu\text{m}$) decreased from onshore to offshore stations, ranging from ~35.74% at PM7 and ~13.13% at C3a, to ~4.76% at SEATs.

As the dominant phytoplankton fraction in SCS, the three major groups of pico-phytoplankton were differently distributed. *Synechococcus* abundance ranged from 1.4×10^4 to 9×10^4 cells ml^{-1} and was most abundant in coastal and continental shelf waters; *Prochlorococcus* was not found at the coastal station (PM7) and its highest abundance (1.8×10^5 cells ml^{-1}) occurred at the oligotrophic oceanic station SEATs; and picoeukaryote abundance ranged from 3.2×10^3 – 1.1×10^5 cells ml^{-1} (Table 2).

The elements and compounds released from the EA aerosol samples are shown in Fig. 2. The aerosol contained a significant amount of seawater leachable N as well as various kinds of trace metals, especially Pb, Zn, Cu, and Fe. The leachable N/P ratio was about 58, 3.6 times higher than the Redfield ratio.

3.2 Phytoplankton size shifts characterized by Chl *a* concentrations

Addition of atmospheric aerosol leachate induced an increase of total Chl *a* and shifted the size structure of phytoplankton across all experiments during the 3 or 4-day of on-deck incubations (Fig. 3). The responses of size-fractionated Chl *a* to the one-time initial aerosol additions were highly consistent at all 3 stations (Experiment 1; Fig. 3a–c). In the High treatment, total Chl *a* concentrations increased significantly by 1.6, 2.5 and 3.5-fold of the control values, with 2.3, 2.9 and 5.6-fold increases of the micro-sized cells and 0.9, 2.3 and 3.4-fold increases of the pico- and nano-sized cells at coastal station PM7, shelf station C3a and oceanic station SEATs, respectively. In contrast to high aerosol additions, low aerosol amendments induced slightly lower Chl

BGD

8, 6637–6680, 2011

Effect of aerosol input on phytoplankton community structure

C. Guo et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

a concentrations by 0.9, 0.8 and 0.9-fold of the control values, with the loss of pico- and nano-sized Chl *a* accounting for the majority of total Chl *a* decline. Compared with Experiment 1, a more dramatic accumulation of total Chl *a* and phytoplankton size shifts were found in the High treatment in Experiment 2, in which aerosol leachate was added daily during the incubation period (Fig. 3d). The concentration of total Chl *a* was enhanced 5.5-fold, with micro-sized cells increasing 14.7-fold relative to the control. The Chl *a* concentration in the Low treatment also showed a slight increase, which is different from Experiment 1. In Experiment 3, the addition of aerosol leachate resulted in a larger increase in Chl *a* concentration, when compared with the control and other 3 treatments (Fig. 3e). A smaller increase was observed in the N+P treatment during the 3-day incubation compared with the control. No significant differences were observed between control bottles and those enriched with N+Si and P+Si. Chl *a* concentrations measured by fluorometry were consistent to those obtained by HPLC.

3.3 Phytoplankton assemblage shifts characterized by phytopigments

In addition to size-fractionated Chl *a*, a further 18 different types of pigments were analyzed by HPLC to determine the contribution of different phytoplankton communities in response to aerosol amendments. Changes in 13 typical phytoplankton markers chlorophylls and carotenoids are demonstrated in Fig. 4. A remarkable increase of fucoxanthin, the marker pigment for diatoms, could be clearly observed in C3a, S412 and A1 in the High treatments (Fig. 4a–b). Shifts in the phytoplankton community composition were also revealed by different degrees of increases in some minor phytoplankton groups as indicated by their marker pigments, such as peridinin, Chl *c*2, diadinoxanthin and β -carotene (dinoflagellates), 19'-hexanoyloxyfucoxanthin (prymnesiophytes, including *coccolithophores* and some picoeukaryotes), neoxanthin and Chl *b* (green alga). In the Low treatments, no apparent change or even a slight decline was observed in the pigment concentrations when compared with the control during incubations. On the other hand, zeaxanthin, the marker pigment of cyanobacteria (including *Prochlorococcus* and *Synechococcus*), was the only pigment that decreased

Effect of aerosol input on phytoplankton community structure

C. Guo et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



or generally remained constant in the High treatment at C3a and S412 (Fig. 4a, c). In Experiment 2, the daily aerosol enrichment induced a more remarkable increase of some pigments, such as neoxanthin by 15.6-fold and fucoxanthin by 7.8-fold in the High treatment (Fig. 4c). In Experiment 3, most phytopigments showed the strongest positive response to aerosol addition, and the second strongest reaction to N+P enrichment (Fig. 4d).

3.4 Group specific responses of picophytoplankton

Flow cytometric measurements showed that picoplankton populations of *Prochlorococcus*, *Synechococcus* and picoeukaryotes did not respond uniformly to the EA aerosol leachate (Fig. 5). In Experiment 1 and 2, the abundance of *Prochlorococcus* and *Synechococcus* displayed a small increase in the Low treatments, while they showed either no change or a decrease in the High treatments when compared with the control at most stations (Fig. 5a–b, d, f, h). However, at oceanic station SEATs, the responses of *Prochlorococcus* and *Synechococcus* in the High treatment were significant with approximately a 2-fold increase when compared with the control (Fig. 5c, g). These results are consistent with the change of zeaxanthin concentrations measured by HPLC (Fig. 4). The abundance of picoeukaryotes showed increases in both the Low and High treatments by 1.1–1.8 and 1.7–3.4 times the control values, respectively, during incubation (Fig. 5j–m).

The comparison of picoplankton responses to various nutrient species also indicated different nutrient requirements between groups as presented in Experiment 3 (Fig. 5e, i, n). Significant increases in the abundance of *Prochlorococcus* and *Synechococcus* were observed in the aerosol and N+P treatments. For picoeukaryotes, all four treatments induced a higher abundance when compared with the control, with the addition of aerosol and N in combination with P or Si resulting in larger increases.

BGD

8, 6637–6680, 2011

Effect of aerosol input on phytoplankton community structure

C. Guo et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

3.5 Group specific responses of microplankton

Total micro-phytoplankton abundance increased significantly by 3.8, 1.7, and 1.8-fold respectively at PM7, C3a and SEATs in Experiment 1, and 9.1-fold at S412 in Experiment 2 (Fig. 6a–d). Diatoms were dominant in the assemblage, with 4.1, 1.7, 2.0-fold increases after high aerosol addition at PM7, C3a and SEATs respectively in Experiment 1, and 9.4-fold at S412 in Experiment 2. *Chaetoceros* spp., *Pseudonitzschia* spp., *Guinardia* spp., *Thalassionema* spp., and *Skeletonema* spp. were the dominant species of diatoms, and their abundances were strongly promoted by the aerosol additions (Fig. 6e–h). Accounting for only a minor percentage in the assemblage, abundances of dinoflagellates species showed a decreasing trend after aerosol addition, which was in contrast to diatoms (Fig. 6i–l).

The protist grazers exhibited significant increases after addition of aerosol (Fig. 7). The abundance of HNF increased by about 1.3- and 1.8-fold on average respectively in the Low and High treatment in Experiment 1 and 2, and the abundance of ciliate also showed increases (Fig. 7a–d and f–h). In Experiment 3, the abundance of HNF increased significantly by 2, 1.9, 1.6-fold in the aerosol, N+P and N+Si treatment, respectively (Fig. 7e).

3.6 Physiological characters

Some statistically significant physiological changes were observed after aerosol enrichment incubations. These changes included enhancement of photosynthetic efficiency, quick utilization of nutrients (data not shown), and an increase of cellular and community biomass as indicated by significantly enhanced cytometric signal of side scatter and red fluorescence signal (Figs. 8–10). The Fv/ Fm ratio, which has been interpreted as indicative of nutrient stress (Olaizola et al., 1996), showed higher values in the High treatment at stations PM7 and S412 compared with the controls (Fig. 8). Enhancement of side scatter and Chl fluorescence was consistently observed across all experiments for *Prochlorococcus* and *Synechococcus* after high aerosol addition, whereas

BGD

8, 6637–6680, 2011

Effect of aerosol input on phytoplankton community structure

C. Guo et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

no significant differences were found between most of the Low treatments and the controls (Figs. 9 and 10). On the contrary, for picoeukaryotes, lower cellular Chl *a* and carbon contents occurred in both the Low and High treatments (Figs. 9 and 10).

4 Discussion

4.1 Unique features of the EA aerosol: its capacity/potential of relieving nutrient limitation in SCS

As a significant nutrient source for marine ecosystems, the atmospheric aerosol depositions from different origins are diverse in composition and size ranges. For example, Saharan aerosol which is originated from Saharan desert and carried over to the western Mediterranean Sea was reported to be coarse in grain size, and served as an important source of soluble P to the West Mediterranean region (Ridame and Guieu, 2002). However, the EA aerosol has a much broader fine-size mass distribution contributed by industrial sources on the Chinese eastern coast, and is a good supplier of N rather than P (Fig. 2; Duce et al., 1991; Chameides et al., 1999; Cohen et al., 2004). Compared with African and European aerosols, the EA aerosol samples we used contain notably higher contents of most trace metal elements, especially Cd, Pb, Cu, Zn and Fe, which are approximately 4–50 times higher than those in African and European aerosols (Paytan et al., 2009). For the macronutrients, NH_4^+ concentration in the EA aerosol sample is estimated to be 8 times higher than that in African and European aerosols, but NO_3^- is a little lower in our EA aerosol sample compared with African and European aerosols (Paytan et al., 2009).

Regional variations of atmospheric deposition may have significant impact on spatial patterns of phytoplankton assemblages and thus biogeochemical cycles. Studies that investigated the effect of aerosol input on marine ecosystems in different regions using enrichment bioassay methods have been done in the Red Sea, Mediterranean Sea, North Atlantic Ocean and high mountain lakes using Sahara dust or European aerosols

BGD

8, 6637–6680, 2011

Effect of aerosol input on phytoplankton community structure

C. Guo et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Effect of aerosol input on phytoplankton community structure

C. Guo et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[⏪](#)[⏩](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

in recent years, as summarized in Table 3. The approximate doses of aerosol we added in our experimental treatments are lower than the amount used in several recent microcosm studies (Table 3), and correspond to the expected range that can occur in the ocean during large deposition events. A pronounced enhancement of Chl *a* (per mg aerosol) was obtained in the High treatment of our study, in which $\sim 1.23\text{--}1.97\ \mu\text{g l}^{-1}$ Chl *a* was developed per mg aerosol in 3 or 4 days, indicating the strong ability of EA aerosols in stimulating phytoplankton biomass accumulation due to its anthropogenic nature.

It has been suggested that, in the oligotrophic South China Sea, phytoplankton growth was limited by nutrient availability, especially N and Fe (Wu et al., 2003; Chen et al., 2004). During this cruise, N/P ratios larger than 16 were observed at most of the stations, supporting the point that N was relatively limited in this ecosystem (data provided by Dai, M.). In our Experiment 3, the increase of biomass induced by the N+P or N+Si addition were far less than that induced by aerosol addition (N/P ratio is ~ 58), suggesting that the limitation of some trace elements other than N+P occurred simultaneously. The high level of trace metals released by the aerosol, possibly Fe, together with N released from the EA aerosol, was inferred to be the most probable reason for the pulse of biomass in the aerosol treatment, because it has been reported that the Fe concentration in SCS was only about 0.2–0.3 nM, which is similar to those in the central North Pacific (Wu et al., 2003). It is also possible that other aerosol-derived components (e.g. trace metals other than Fe, organic nutrients) introduced by aerosol or synergistic interactions between different elements served an important role in the process.

4.2 Negative response on bulk phytoplankton biomass to low aerosol addition: possibility of enhanced grazing

In addition to the stimulating effect of aerosol-derived nutrient supply on phytoplankton growth, the cell removing process promoted by aerosol nutrients should also be taken into account when interpreting the bioassay experiment. In Experiment 1, we observed

a slight decline of total Chl *a* concentration induced by a low amount of EA aerosol addition, which was inconsistent with the previous result of linear increase of Chl *a* with increasing concentration of fresh Saharan dust addition that was demonstrated by Herut et al. (2005). At the same time, the abundance of HNF increased significantly in the

5 Low treatment. We also measured total bacterial abundance from the same study, and correlation analysis showed that the total bacterial and HNF abundances were negatively correlated at some stations (Guo et al., 2011). So it is reasonable to suspect that the lack of biomass accumulation was probably attributed to protistan grazing, which has been well established as a significant and even dominant source of mortality for phytoplankton (from small picophytoplankton to large chain-forming diatoms), bacteria and other protists in aquatic microbial food webs (Sherr and Sherr, 2002). Nutrient enrichment can cause a quick improvement in the physiological characters (e.g. increase of cell size and cellular Chl *a* content) of phytoplankton cell (Cavender-Bares et al., 2001) and consequently stimulate microzooplankton grazing on prey with improved food quality (Landry et al., 2000; Worden and Binder, 2003). Therefore, it is possible that low level of aerosol enrichment was not sufficient to cause phytoplankton biomass accumulation, but instead it resulted in enhanced grazing loss due to improved cellular physiology in this study. Such phenomenon has also been observed in other studies (e.g. Romero et al., 2010) and can also affect phytoplankton community structures and physiological characters (see Figs. 3–8).

4.3 Different responses of pico- and micro-phytoplankton and among different taxa: inhibition and stimulation effect

There was a clear change in phytoplankton assemblage in response to the EA aerosol enrichment (see Figs. 2–4). Generally, phytoplankton of all size fractions were stimulated, but the effect on picoplankton was not as pronounced as that on microplankton (Figs. 3 and 5–6), inducing a phytoplankton size and composition shift. According to both pigment and microscopic data, the large diatoms and haptophytes were promoted the most by aerosols. This result is consistent with the observations of many

Effect of aerosol input on phytoplankton community structure

C. Guo et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



iron enrichment experiments which showed that diatoms become the dominant phytoplankton after the addition of iron (Hutchins et al., 1998; Boyd et al., 2007), due to the ability of better equipped and rapid response to injections of new nutrients (Goldman, 1993; Zubkov et al., 1998) and escape of grazing pressure (Boyd et al., 2007). With the influence of aerosol nutrients, it has been suggested that diatom species succession follows abundance of different diatom species increasing by different degrees. The prevalent species after aerosol addition, e.g. *Chaetoceros* spp., *Pseudonitzschia* spp., *Guinardia* spp., *Thalassionema* spp., and *Skeletonema* spp., are all diatoms associated with high growth rates under enhanced nutrient availability. It has also been indicated that the episodic atmospheric deposition could lead to the reserve of Fe within the large cells when their growth is co-limited by Fe and another factor, e.g. N in SCS (Blain et al., 2004). However, growth of dinoflagellates was not fueled by the aerosol, possibly because they were outcompeted by diatoms.

Oceanic small autotrophs are more capable of meeting their cellular Fe demand in low Fe environments than larger eukaryotic species such as diatoms (DiTullio et al., 1993), and are expected to favor nutrient-limited ecosystems (Chisholm, 1992; DiTullio et al., 1993; Raven 1998). In the oligotrophic SCS, the smallest organisms e.g. picocyanobacteria, dominated the autotrophic assemblages, and they were not strongly affected by EA aerosol. The three picoplankton groups displayed very different preferences to the aerosol enrichment due to their different physiological and genetic features. Generally, *Prochlorococcus* and *Synechococcus* do not benefit from high concentrations of aerosol leachate, possibly because they have minimized their genome during evolution and lack the ability to produce proteins responsible for nutrient-uptake regulation (Dufresne et al., 2003; Rocap et al., 2003). The cyanobacteria have also been reported to be particularly sensitive to some trace metals. For instance, the growth and cell division of *Synechococcus* could be severely inhibited in the copper-contaminated environment with free $[Cu^{2+}] > 10^{-12} \text{ mol l}^{-1}$ (Brand et al., 1986; Bruland et al., 1991; Moffett and Brand, 1996; Mann et al., 2002). Paytan et al. (2009) have observed that the threshold toxicity of Cu is $0.2\text{--}2 \mu\text{g}/(\mu\text{g Chl } a)^{-1}$, while, in our study,

BGD

8, 6637–6680, 2011

Effect of aerosol input on phytoplankton community structure

C. Guo et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



the concentration was $0.5\text{--}3\ \mu\text{g}/(\mu\text{g Chl } a)^{-1}$, which is in or above their threshold toxicity. Both unfavorable macronutrient level and aerosol-derived trace metal toxicity may have contributed to the negative effect on *Prochlorococcus* and *Synechococcus*. The results of Experiment 3 showed lower *Prochlorococcus* abundance in aerosol treatment than the N+P treatment with the same concentrations of inorganic N, which suggest more important roles of trace metals or other elements played in inhibiting *Prochlorococcus* growth. Consistent with our experiment at the shelf station C3a, declines in the *Prochlorococcus* community have also been observed in Mediterranean waters, Red Sea and Atlantic Ocean in response to Sahara dust and African aerosols (Herut et al., 2005; Payan et al., 2009; Marañón et al., 2010; see Table 3). Abundance of picoeukaryotes increased significantly, suggesting their increased ability to adapt to nutrient replete environments compared with picocyanobacteria.

4.4 Aerosol effects on physiological states of phytoplankton

The physiological variables of phytoplankton populations in SCS also demonstrated a marked response to the EA aerosol input. The cellular carbon content can indicate the cell energy content, and cellular Chl *a* content reflected by relative red fluorescence can imply the cell energy supply ability (Geider, 1987). Here, for *Prochlorococcus*, *Synechococcus* and picoeukaryotes, cellular carbon content and cellular Chl *a* content both exhibited immediate and significant enhancement after high aerosol addition in all experiments, indicating that physiological stress was relieved by aerosol nutrients. Such responses are consistent with the high N requirement and low P requirement for the synthesis of pigment-protein macromolecular complexes (Geider and La Roche, 2002). Enhanced microzooplankton grazing mortality, selective ingestion in favor of cells of a larger size and higher nutrient content (Gonzalez et al., 1990; Sherr and Sherr, 1994; Worden and Binder, 2003), or prevalence of small species of picoeukaryotes are the most likely reason for the observed cellular carbon and Chl *a* decrease of picoeukaryotes in the Low treatment. The ability of alleviating nutrient limitation by

BGD

8, 6637–6680, 2011

Effect of aerosol input on phytoplankton community structure

C. Guo et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

the EA aerosol can also be demonstrated by the significantly higher photochemical efficiency of PSII (Fv/Fm) after high aerosol addition (Kolber et al., 1988, 1994; Greene et al., 1992; Berges et al., 1996).

4.5 Ecological and biogeochemical implications and future prospects

5 The shift of phytoplankton biomass, size and species composition in response to the high level of EA aerosol has broad implications for the understanding of atmosphere-ocean interactions in SCS from a biogeochemical point of view. As a typical oligotrophic subtropical marginal sea of the North Pacific, SCS is viewed as a weak carbon source (Zhai et al., 2005). The community structure, especially the size structure
10 of the primary producers and the microbial food web, plays a very important role in determining the oceanic carbon flux (Zhai et al., 2005). In SCS, the phytoplankton community is dominated by picophytoplankton, which contribute less to direct vertical export due to the small size and low sinking rate (Hagstrom et al., 1988; Lomas and Moran, 2011). Diatoms, though make up only a small fraction of the total phytoplankton
15 production, are responsible for the majority of export production in open ocean environments (Smetacek, 1985; Goldman, 1993; Buesseler, 1998). Since a large amount of aerosol loading results in the bloom of large phytoplankton (especially diatoms) it can shift the phytoplankton to a large cell dominated community and potentially enhance the export fluxes of carbon through sinking of senescent cells (Miller et al., 1991; Goldman, 1993; Boyd et al., 1998). At the same time, the aerosol enrichment also enhances the physiological conditions of the autotrophs, and may stimulate zooplankton grazing activities, which may also increase the carbon export through downward fluxes of fecal pellets. Both the structural and physiological shifts are likely to result in elevated vertical carbon export, drawdown of $p\text{CO}_2$ and finally change the carbon budget in SCS.
25 Besides the autotrophic phytoplankton, we also observed obvious changes in bacteria composition (Guo et al., 2011), as well as significant increase of protist abundance, further indicating the potential effect of the EA aerosol to the biogeochemical cycle in SCS. However, the effect of aerosol on marine ecosystem could be highly variable

Effect of aerosol input on phytoplankton community structure

C. Guo et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



real conditions may not be as strong as during the in vitro experiments. Nevertheless, Romero et al. (2010) reported that dust inputs accompanied by turbulence might magnify the effects. In our case, considering the intense and large-scale of the northeast monsoon in winter and oligotrophic nature of SCS, we believe that the loading of highly anthropogenic-derived EA aerosol plays an important role in potentially affecting the primary production, planktonic food web dynamics, and carbon flux in SCS.

5 Conclusions

In summary, our study demonstrated for the first time the detailed interactions between EA aerosol deposition and marine phytoplankton community dynamics in SCS. Generally, the EA aerosol deposition enhances the photosynthetic rate and biomass and shifts the dominant taxa of phytoplankton assemblages from picophytoplankton to microphytoplankton, especially large diatoms. Picocyanobacteria, *Prochlorococcus* and *Synechococcus*, showed sensitivity to the EA aerosols and their growths were inhibited when the aerosol addition was high in most experiments. Under high levels of aerosol loading, the phytoplankton composition shift was apparent, with cellular physiological conditions remarkably improved and more Chl *a* and carbon biomass accumulated. However, under low levels of aerosol loading, the composition shift was less remarkable and biomass accumulation was not apparent, suggesting that the stimulation of phytoplankton growth by bioavailable nutrients in the aerosol is counterbalanced by increased biomass loss, possibly due to enhanced grazing mortality. Moreover, continuous atmospheric deposition could lead to a more conspicuous effect compared to episodic short-time atmospheric events. In coastal regions, the EA aerosol induced a strong assemblage shift toward diatoms, which may promote an algal bloom; while in oceanic regions, the aerosol resulted in a pronounced increase of phytoplankton biomass, which may enhance the efficiency of the biological pump. Therefore, a better understanding of the impact of nutrient inputs from EA aerosols on the marine photosynthetic community and its ecological and biogeochemical consequences are crucial for predicting the oceanic carbon cycle in the climate change models.

Effect of aerosol input on phytoplankton community structure

C. Guo et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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Effect of aerosol input on phytoplankton community structure

C. Guo et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



**Effect of aerosol
input on
phytoplankton
community structure**

C. Guo et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

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Effect of aerosol input on phytoplankton community structure

C. Guo et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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Effect of aerosol input on phytoplankton community structure

C. Guo et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Res. I, 40, 159–168, 1993.

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Effect of aerosol input on phytoplankton community structure

C. Guo et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Jickells, T. D., An, Z. S., Andersen, K. K., Baker, A. R., Bergametti, G., Brooks, N., Cao, J. J., Boyd, P. W., Duce, R. A., Hunter, K. A., Kawahata, H., Kubilay, N., Laroche, J., Liss, P. S., Mahowald, N., Prospero, J. M., Ridgwell, A. J., Tegen, I., and Torres, R.: Global iron connections between desert dust, ocean biogeochemistry, and climate, *Science*, 308, 67–71, 2005.

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Effect of aerosol input on phytoplankton community structure

C. Guo et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Effect of aerosol input on phytoplankton community structure

C. Guo et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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Effect of aerosol input on phytoplankton community structure

C. Guo et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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Effect of aerosol input on phytoplankton community structure

C. Guo et al.

Table 1. Description of aerosol and inorganic nutrient enrichment experiments.

Experiment	Station	Treatment	Addition
Exp 1: Initial aerosol enrichment bioassay	PM7, C3a SEATs	Control	None
		Low	AL: 0.5 ml
		High	AL: 5.0 ml
Exp 2: Everyday aerosol enrichment bioassay	S412	Control	None
		Low	AL: 0.2 ml day ⁻¹
		High	AL: 2.0 ml day ⁻¹
Exp 3: Aerosols and chemical nutrients enrichment bioassay	A1	Control	None
		Aerosol	AL: 5.0 ml
		N+P	[NH ₄ NO ₃] 0.5 μM + [PO ₄ ³⁻] 0.1 μM
		N+Si	[NH ₄ NO ₃] 0.5 μM + [SiO ₃ ²⁻] 1 μM
P+Si	[PO ₄ ³⁻] 0.1 μM + [SiO ₃ ²⁻] 1 μM		

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Effect of aerosol input on phytoplankton community structure

C. Guo et al.

Table 2. Initial conditions for bioassay experiments.

Station	PM7	C3a	SEATs	A1	S412
Type of location	coastal	continental shelf	oceanic	continental shelf	oceanic
Bottom depth (m)	17	137	3844	854	3340
Surface Temperature (°C)	25.40	22.82	24.66	23.27	24.27
Salinity	34.30	34.06	33.72	34.07	33.80
NO ₂ ⁻ + NO ₃ ⁻ (μmol l ⁻¹)	1.020	0.609	< 0.100	0.244	< 0.100
PO ₄ ³⁻ (μmol l ⁻¹)	0.120	< 0.080	< 0.080	0.082	< 0.080
SiO ₃ ²⁻ (μmol l ⁻¹)	2.550	1.504	2.406	1.175	1.75
[Chl <i>a</i> >20 μm] (μg l ⁻¹)	0.161(0.020)	0.041(0.003)	0.004(0.001)	0.032(0.004)	0.035(0.001)
[Chl <i>a</i> <20 μm] (μg l ⁻¹)	0.289(0.045)	0.268(0.003)	0.077(0.011)	0.248 (0.044)	0.427(0.020)
[Chl <i>a</i> total] (μg l ⁻¹)	0.450(0.065)	0.309(0.001)	0.081(0.013)	0.281 (0.041)	0.462(0.022)
[>20 μm Chl <i>a</i>]%	36 %	13 %	5 %	11 %	8 %
<i>Prochlorococcus</i> (cells ml ⁻¹)	0	40 731(271)	178 497(6545)	21 241(1157)	23 576(1952)
<i>Synechococcus</i> (cells ml ⁻¹)	93 694	46 980(795)	14 183(142)	25 580(322)	49 747(1704)
Picoeukaeyotes (cells ml ⁻¹)	5304	5577(234)	3225(124)	5145(18)	11 552(957)

The numbers in parenthesis are standard errors of the mean.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Effect of aerosol input on phytoplankton community structure

C. Guo et al.

Title Page

Abstract Introduction

Conclusions References

Tables Figures

◀ ▶

◀ ▶

Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Table 3. Recent studies of the effect of aerosol input on marine ecosystems in different regions using the enrichment bioassay method.

Region	Hydrotrophic features	Material	Addition (mg l ⁻¹)	Chl response	Response of autotrophic communities			Explanation	Reference		
					Pico abund.					Micro-abund.	Nano-abund.
					Pro	Syn	Peuk				
Red Sea	N, P co-limitation	European aerosol	0.75	↑2–fold	→	↑	↑	Aerosol can induce both fertilization effect (N and P) and toxicity effect (Cu)	Paytan et al. (2009)		
		African aerosol	0.75	↓	→	↓	↓				
Eastern Mediterranean	ultra-oligotrophic	Fresh Sahara dust	4.88	↑4.76–fold	↓	↑	↓	Nutrient released from dust triggered the primary production enhancement	Herut et al. (2005)		
		Pre-leached dust	4.75–4.94	→	↓	↑	↓			↓	
Mediterranean coast	sampled during a bloom; P limitation	Sahara dust	500	↑3.3–fold	↓	↑	↑	P and other nutrients in Sahara dust have a fertilization effect.	Lekunberri et al. (2010)		
			50	↑1.5–fold	↓	↑					
Northwest Mediterranean	well stratified; low-nutrient low- Chl	Sahara dust	0.25	→	benefit eukaryotic populations			Atmospheric supply of nutrients during stratified period significantly altered the community structure	Bonnet et al. (2005)		
		Anthropogenic particles	0.01	↑	enhance mainly pico- and nano-phytoplankton						
Northeast Atlantic	variable properties; intermediate DFe conc.	Sahara dust	1.34	↑<2–fold	↑	↑	→	Sahara dust supply bioavailable Fe and relieve Fe limitation	Blain et al. (2004)		
Tropical North Atlantic	oligotrophic; N limitation	Sahara surface soils	0.5/2	↑or →	dust relieve P and Fe co-limitation of diazotrophy in the region			Saharan dust addition stimulated nitrogen fixation by supplying both Fe and P.	Mills et al. (2004)		
Central North Atlantic	oligotrophic; nutrient limitation	Sahara soils/aerosol	2	↑	biological responses were similar to Fe addition			Fe supplied by dust increases the rate of nitrate consumption, which is important in controlling the dynamics of spring bloom	Moore et al. (2006)		
Central Atlantic	oligotrophic	Sahara dust	2	↑	↓	↓	↑	↑	The response of microbial plankton depends on the ecosystem's degree of oligotrophy and was modulated by the competition of nutrients between phytoplankton and heterotrophic bacteria.	Maranon et al. (2010)	
Northwest Mediterranean coast	After spring bloom; P limitation	Sahara dust	50	→			↑	Dust pulses occurring after spring bloom can regenerate the bloom, and change the phytoplankton dynamics.	Romero et al. (2011)		
			500	↑10–fold			↑				

↑: Increase; ↓: decrease; →: no significant change; abund.: abundance.



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Effect of aerosol input on phytoplankton community structure

C. Guo et al.

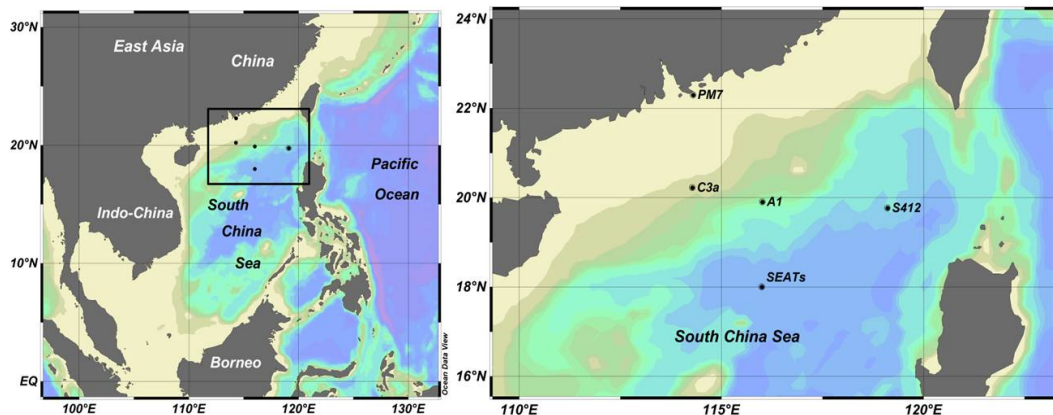


Fig. 1. Locations of the stations where the microcosm bioassay experiments were performed.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[⏪](#)[⏩](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

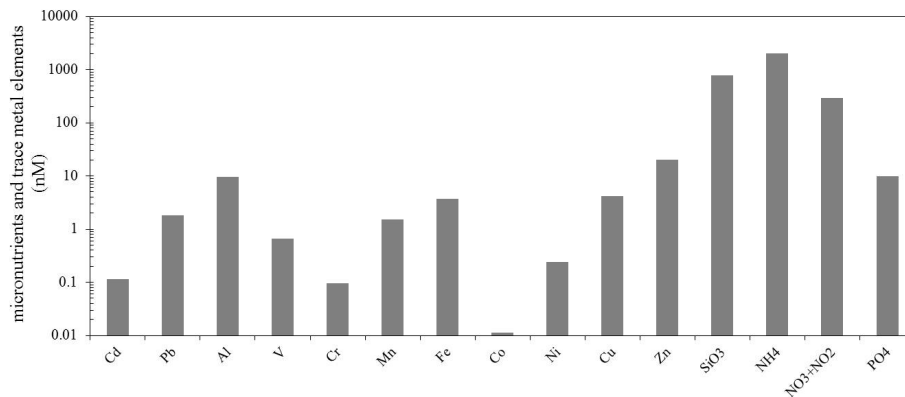


Fig. 2. Enrichment of trace metal element and macro-nutrient (nM) from the addition of East Asia aerosol leachate. The amounts were released to the incubation bottles of High treatment in Experiment 1 and Aerosol treatment in Experiment 3 from the addition of 5 ml aerosol leachate.

Effect of aerosol input on phytoplankton community structure

C. Guo et al.

Title Page

Abstract Introduction

Conclusions References

Tables Figures

⏪ ⏩

◀ ▶

Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Effect of aerosol input on phytoplankton community structure

C. Guo et al.

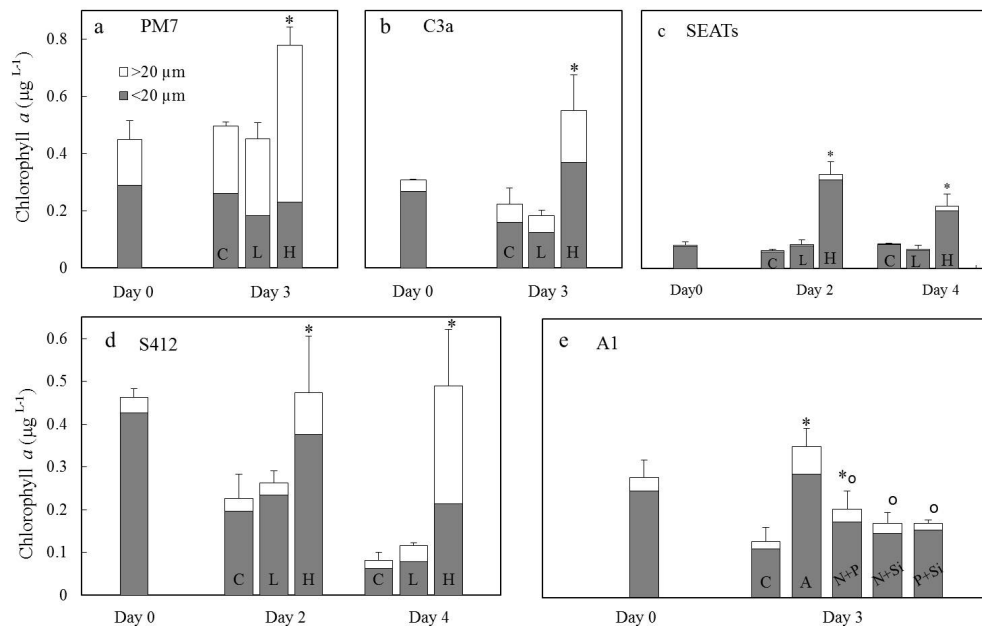


Fig. 3. Response of Chl *a* concentrations in the South China Sea to the addition of EA aerosols and inorganic nutrients. **(a–c)** Experiment 1, **(d)** Experiment 2, and **(e)** Experiment 3. Error bars represent the standard deviation of total Chl *a* concentration from triplicate incubations. Asterisks indicate statistically significant mean Chl *a* values ($p < 0.05$) of treatments compared with the controls on day 3. Circles indicate significant mean Chl *a* values ($p < 0.05$) of treatments compared with treatment A on day 3 in **(e)**. C: Control; L: Low treatment; H: high treatment; A: aerosol treatment (see Table 1).

Title Page

Abstract Introduction

Conclusions References

Tables Figures

◀ ▶

◀ ▶

Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Effect of aerosol input on phytoplankton community structure

C. Guo et al.

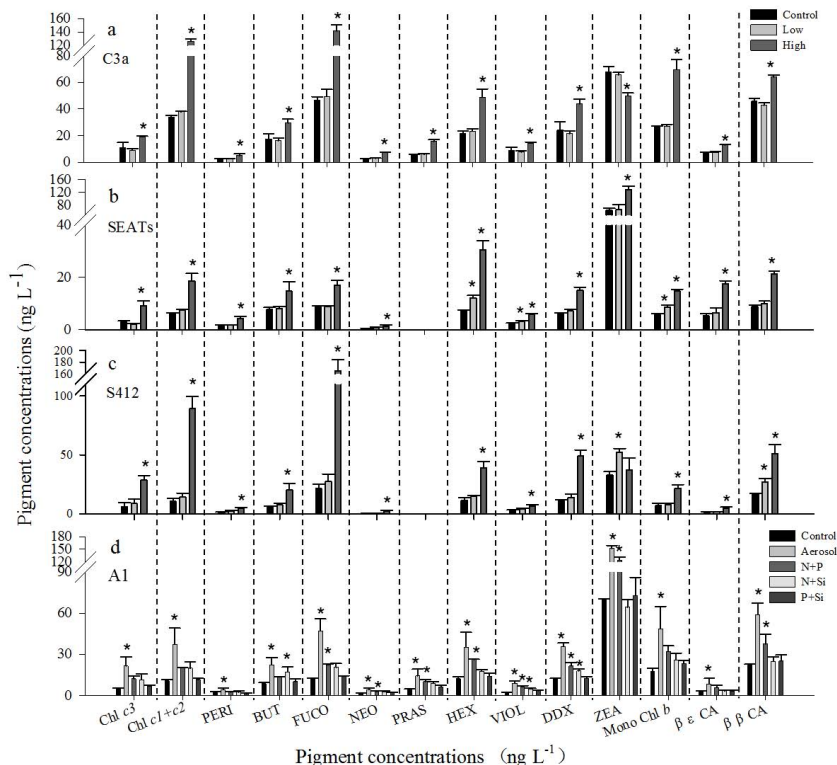


Fig. 4. Responses of 14 kinds of phytopigments to aerosol and inorganic nutrient enrichment at (a) C3a and (b) SEATs of Experiment 1, (c) S412 of Experiment 2, and (d) A1 of Experiment 3. Error bars represent the standard deviation from triplicate incubations. Asterisks indicate statistically significant mean values ($p < 0.05$) compared with the controls. Chl c3: Chl c3; chl c1+c2: Chl c1+c2; PERI: Peridinin; BUT: 19'-butanoyloxyfucoxanthin; FUCO: Fucoxanthin; NEO: Neoxanthin; PRAS: Prasincoxanthin; HEX: 19'-hexa-noyloxyfucoxanthin; VIOL: Violaxanthin DDX: Diadinoxanthin; ZEA: Zeaxanthin; Mono Chl b: Monovinyl chlorophyll b; $\beta\epsilon$ CA: β,ϵ -Carotene; $\beta\beta$ CA: β,β -carotene.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Effect of aerosol input on phytoplankton community structure

C. Guo et al.

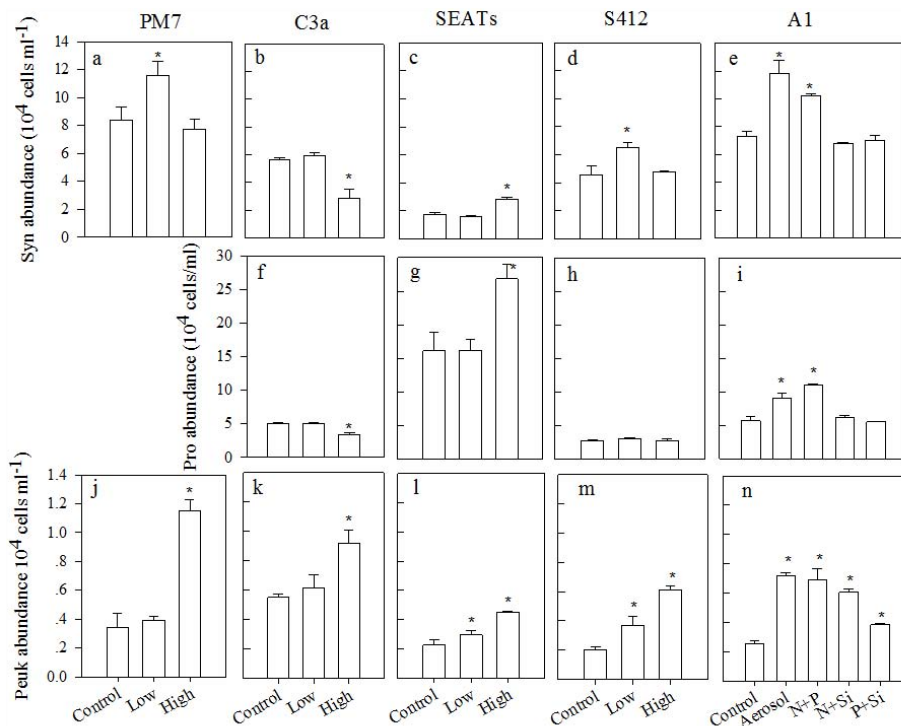


Fig. 5. Response of picoplankton abundances to the EA aerosol enrichment. The abundances of (a–e) *Synechococcus* (Syn), (f–i) *Prochlorococcus* (Pro), and (j–n) picoeukaryotes (Peuk) following control, low or high treatment measured at 48 or 96 h by flow cytometry. Error bars represent the standard deviation from triplicate incubations. Asterisks indicate statistically significant mean values ($p < 0.05$) compared with the controls.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Effect of aerosol input on phytoplankton community structure

C. Guo et al.

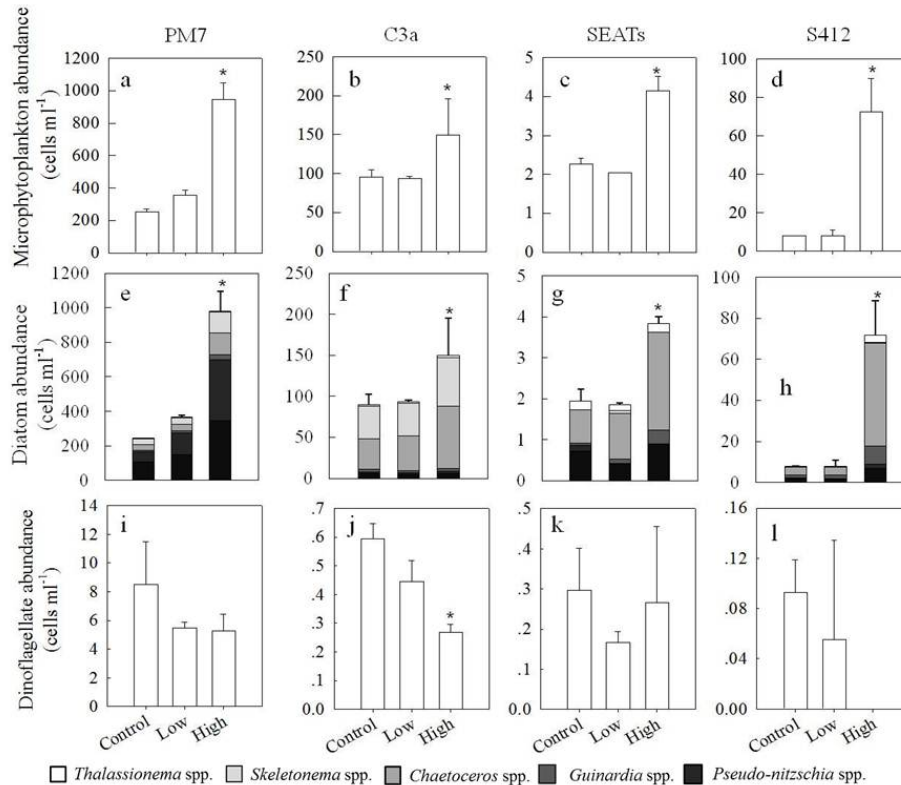


Fig. 6. Response of microplankton abundances to the EA aerosol enrichment. The abundances of (a–e) total microphytoplankton, (f–i) Diatoms, and (j–n) dinoflagellate following control, low or high treatment measured at 96 h by microscope. Error bars represent the standard deviation from triplicate incubations. Asterisks indicate statistically significant mean values ($p < 0.05$) compared with the controls (f–i).

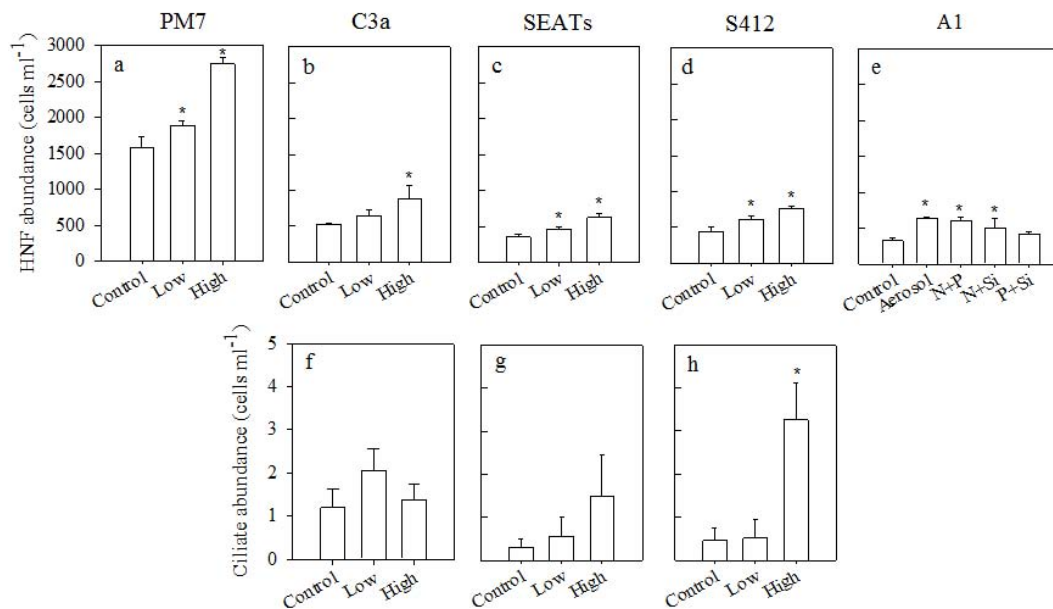


Fig. 7. Response of protistan grazer abundances to the EA aerosol enrichment. The abundances of (a–e) HNF, and (f–h) ciliate following control, low or high treatment measured at 48 or 96 h by flow cytometry. Error bars represent the standard deviation from triplicate incubations. Asterisks indicate statistically significant mean values ($p < 0.05$) compared with the controls.

Effect of aerosol input on phytoplankton community structure

C. Guo et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Effect of aerosol input on phytoplankton community structure

C. Guo et al.

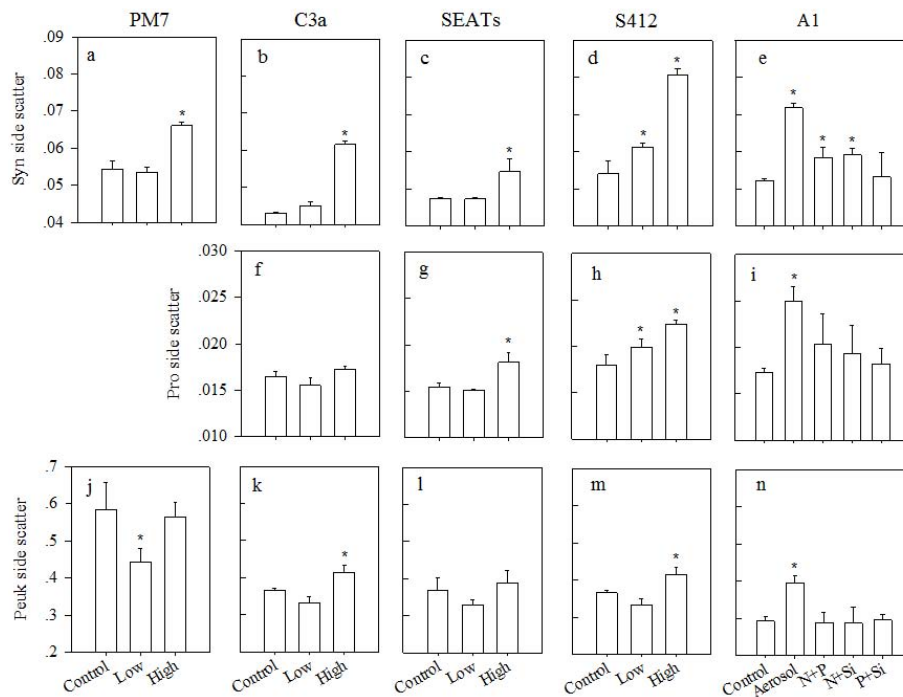


Fig. 8. Response of picoplankton normalized side scatter signal to the EA aerosol enrichment. The abundances of (a–e) *Synechococcus* (Syn), (f–i) *Prochlorococcus* (Pro), and (j–n) picoeukaryotes (Peuk) following control, low or high treatment measured at 48 or 96 h by flow cytometry. Error bars represent the standard deviation from triplicate incubations. Asterisks indicate statistically significant mean values ($p < 0.05$) compared with the controls.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Effect of aerosol input on phytoplankton community structure

C. Guo et al.

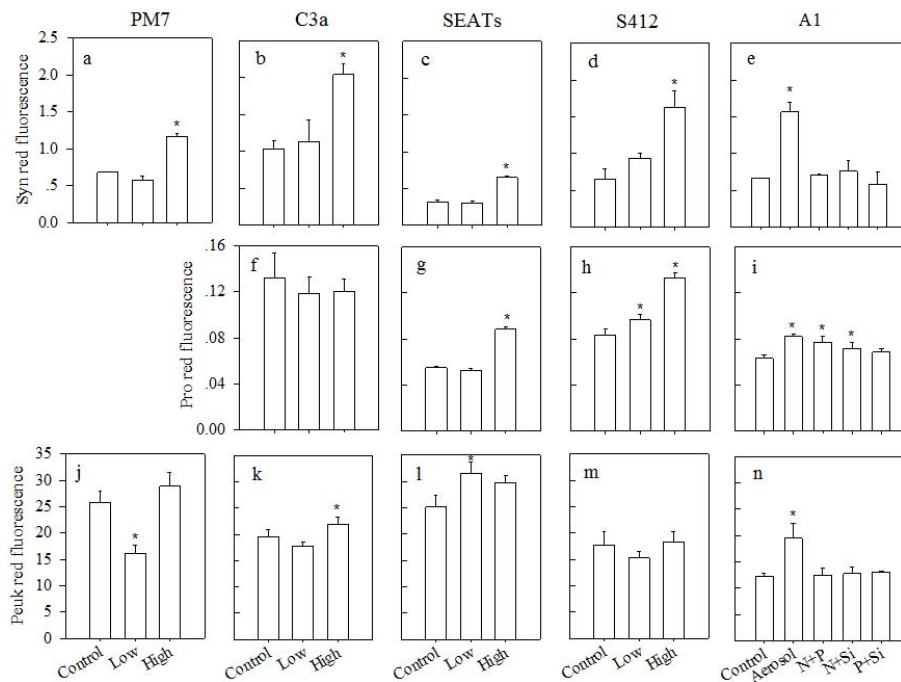


Fig. 9. Response of picoplankton normalized red fluorescence to the EA aerosol enrichment. The abundances of **(a–e)** *Synechococcus* (Syn), **(f–i)** *Prochlorococcus* (Pro), and **(j–n)** picocoeukaryotes (Peuk) following control, low or high treatment measured at 48 or 96 h by flow cytometry. Error bars represent the standard deviation from triplicate incubations. Asterisks indicate statistically significant mean values ($p < 0.05$) compared with the controls.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Effect of aerosol input on phytoplankton community structure

C. Guo et al.

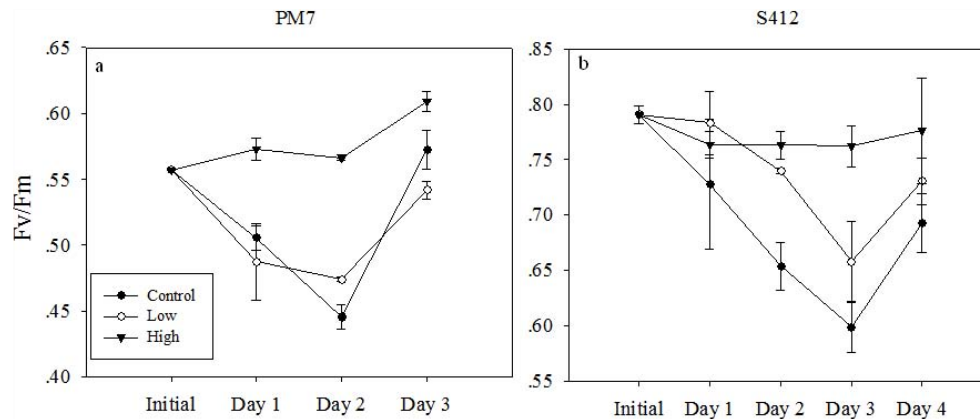


Fig. 10. Phytoplankton photochemical quantum efficiency (F_v/F_m) measured every 24 h at **(a)** PM7 of exp 1 and **(b)** S412 of exp 2. Error bars represent the standard deviation from triplicate incubations.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Effect of aerosol input on phytoplankton community structure

C. Guo et al.

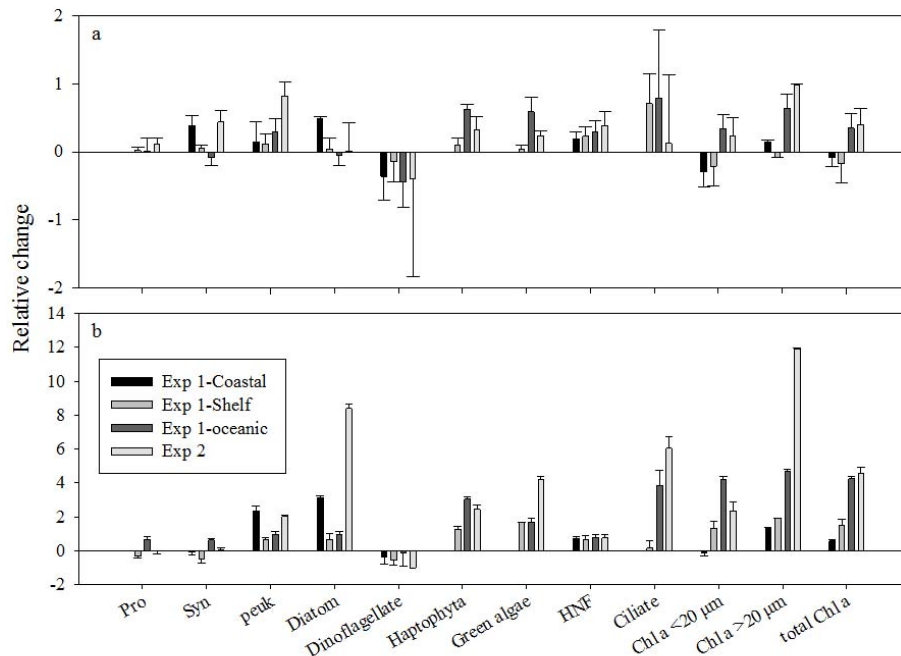


Fig. 11. Responses of Chl *a*, protists and phytoplankton community structure in the Low **(a)** and High **(b)** treatment in Experiment 1 and 2. Relative changes (%) were calculated as $100 \times (A - C) / C$ (A and C are mean values of the variable in the aerosol and control treatments respectively). Error bars represent the propagation of the standard deviation of the measurements in the control and treatments.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion