Environmental Research 278 (2025) 121663

Contents lists available at ScienceDirect

Environmental Research

journal homepage: www.elsevier.com/locate/envres

Diverse dust sources and warming trigger cyanobacteria abundance in freshwater ecosystems in the western United States

Juan Manuel González-Olalla [a,b,1,*], Janice Brahney [b]

[a] Institute of Water Research, University of Granada, Avenida de Madrid, 11, Granada 18071, Spain
[b] Department of Watershed Sciences and Ecology Center, Utah State University, Logan, UT, 84321, USA

ARTICLE INFO

Keywords:
Community composition
Metabolic balance
Nutrients
Phytoplankton
Primary production
Temperature

ABSTRACT

The rise in global temperature and the increase in atmospheric transport and deposition of dust linked to greater aridity, land abandonment, and wildfires, are placing significant stress on freshwater microbial communities. Temperature increases and the nutrients contained in the dust may independently and together alter the metabolism and structure of these communities. However, dust chemistry is widely variable, and pre-existing lake conditions will likely influence the response of the algal and microbial communities to added nutrients and temperature stress. To fill this gap of knowledge, we tested the metabolic and structural response of phytoplankton in two aquatic ecosystems in the Western United States (Half-Moon Lake and Jordanelle Reservoir), which have similar trophic status but different biogeochemical properties, in response to two types of atmospheric dust from the region. The results show that the Temperature × Dust interaction led to greater cyanobacteria growth in Half-Moon compared to Jordanelle. The effect on metabolism also differed, with Half-Moon showing a tendency toward heterotrophy, while Jordanelle trended toward autotrophy. Interestingly, our study reveals that the direction of the response was mainly regulated by each ecosystem's properties, while the magnitude of the response was controlled by the type of dust. Through this work, we demonstrate that oligotrophic freshwater ecosystems are sensitive to dust-nutrient additions leading to cyanobacterial blooms and highlight the importance of considering watershed biogeochemical properties and exposure to different types of dust in lake and reservoir management strategies.

1. Introduction

Recent decades have seen an increase in atmospheric dust emissions due to the expansion of arid areas, the emergence of playas from shrinking lakes, land abandonment, changes in land use, soil disturbance, and wildfires (Dong et al., 2020; Moulin and Chiapello, 2006; Zhou et al., 2023). Dust deposition contributes essential trace elements as well as organic and inorganic nutrients to terrestrial and aquatic ecosystems (Guieu et al., 2002; Jickells et al., 2016). Specifically, dust deposition can enrich oligotrophic ecosystems by providing minerals rich in elements such as phosphorus (P) and iron (Fe) (Brahney et al., 2014; Mahowald et al., 2005). Indeed, studies have shown that dust deposition increases total phosphorus (TP) concentration in waterbodies of the western United States (Brahney et al., 2014, 2015b) and Europe (Morales-Baquero et al., 2006).

The bioavailability of dust elements and their fertilizing capacity on the aquatic microbial community is a compelling area of current research (e.g., Herbert et al., 2018; Li et al., 2022; Weis et al., 2024). Despite the fact that the mean estimated soluble and bioavailable fraction of P in dust is variable (10 % solubility of total P in desert dust, in Stockdale et al., 2016; or 30–45 % in dust collected in Uinta Mountains, United States, in Scholz and Brahney, 2022), its impact on organisms and aquatic ecosystems can be significant given their limitation in this element (González-Olalla et al., 2024; Gross et al., 2020; Villar-Argaiz et al., 2018). Additionally, dust can transport other elements that may alter the chemical composition of freshwater aquatic ecosystems, especially in more sensitive regions (Camarero and Catalan, 2012). For example, a high carbonate content can increase the alkalinity and the concentration of base cations, which are also key nutrients (Brahney et al., 2013; Rogora et al., 2004). In this regard, Pulido-Villena et al. (2006) noted that the atmospheric contribution of P and Ca was essential to explain the functioning of high mountain lakes. Because dust

* Corresponding author.
E-mail address: jmolalla@ugr.es (J.M. González-Olalla).

[1] Present address: Institute of Water Research, University of Granada, Avenida de Madrid, 11, Granada 18071, Spain.

https://doi.org/10.1016/j.envres.2025.121663
Received 8 November 2024; Received in revised form 13 March 2025; Accepted 20 April 2025
Available online 21 April 2025

composition can vary based on the characteristics of the soil and land use it is derived from, its impact on receiving aquatic ecosystems may also vary.

The composition of lake water also plays a crucial role in the bioavailability and impact of dust deposition on aquatic ecosystems. However, the amount of information available for freshwater ecosystems is less compared to marine environments. The heterogeneity of the biogeochemical properties of freshwater ecosystems, in contrast to the relative homogeneity of marine environments, can greatly influence nutrient bioavailability and the community's response to the same dust event (Wen, 2022). For instance, while the pH of the ocean surface shows minimal variation, lakes experience larger pH variations that can affect the degree to which nutrients are released from dust, with low pH levels increasing nutrient availability (González-Olalla et al., 2024).

Beyond the influence of dust on water chemistry and nutrient availability, there are some suggestions that atmospheric phosphorus deposition may influence community composition, including an increase in cyanobacterial presence (Brahney et al., 2015a; Olson et al., 2023), which has implications for water quality as well as ecosystem functioning. In particular, cyanobacterial blooms and their toxins negatively impact food webs, water quality parameters (Brooks et al., 2016), and the stability and functioning of aquatic ecosystems (Havens, 2008). However, there are only a few experiments on how dust deposition affects the structure of freshwater phytoplankton communities (e.g., Wen, 2022). While there is a well-established connection between harmful algal blooms and excess nutrients associated with agricultural, industrial, and urban activities (Paerl et al., 2018), robust information on whether the nutrient inputs contained in dust could lead to the proliferation of such blooms is lacking (Wang et al., 2022). Changes in the composition of phytoplankton communities can also affect biogeochemical cycles and the carbon cycle in aquatic ecosystems (Litchman et al., 2015). Recurrent and/or high-intensity dust deposition events can lead to significant changes in the metabolism and composition of microbial communities in aquatic ecosystems. Dust addition has been shown to stimulate both heterotrophic and autotrophic communities although most of these studies have been conducted in marine environments (e.g. Borchardt et al., 2020; Cabrerizo et al., 2016; Carrillo et al., 2024). This stimulation or inhibition of metabolisms has implications of carbon cycling, shifting ecosystems between net carbon emitters (net heterotrophy) and atmospheric carbon sinks (net autotrophy) (Astrahan et al., 2016; Tsiaras et al., 2017).

In addition to nutrients, temperature is another factor that significantly influences the metabolism and composition of aquatic communities (Brown et al., 2004; Staehr and Sand-Jensen, 2006; Striebel et al., 2016). The increase in temperature associated with global change imposes a continuous stress on aquatic ecosystems, unlike the intermittent nutrient inputs from dust deposition. Elevated temperatures tend to impact heterotrophic metabolism more than autotrophic metabolism, leading to shifts in the net ecosystem productivity (Yvon-Durocher et al., 2010). Additionally, warming can alter community composition, favoring smaller species (Daufresne et al., 2009). There is broad consensus on the stimulating effect of rising temperatures on the proliferation of algal blooms (Paerl and Huisman, 2008; Richardson et al., 2018), particularly cyanobacteria, which gain a competitive advantage in nutrient acquisition (Lürling et al., 2018) and exhibit higher growth rates at elevated temperatures (Butterwick et al., 2005). Moreover, several studies have reported a positive synergistic interaction between temperature and nutrients that favors the proliferation of cyanobacterial blooms (Kosten et al., 2012; Lürling et al., 2018). However, ecological surprises involving antagonistic interactions between these factors have also been reported (Richardson et al., 2019).

This study aims to explore the influence of dust composition, lake water composition, and temperature on phytoplankton community structure and ecosystem metabolism under conditions of global change. To achieve this, we conducted microcosms experiments with aquatic communities sourced from two freshwater aquatic ecosystems in the western United States (Half-Moon Lake and Jordanelle Reservoir) and exposed them to two different types of dust, one with elevated P content and one with elevated carbonate content. Despite these ecosystems sharing a similar oligotrophic trophic state, they differ in their watershed geology with one being in a siliceous basin with lower pH (Half-Moon Lake) and the other in a carbonate/siliceous bedrock with higher pH.

Our hypothesis is threefold: First, we hypothesize that temperature increase and dust inputs will synergistically stimulate heterotrophic metabolism and will favor the predominance of cyanobacteria in the phytoplankton community. Second, we expect that phytoplankton from the more alkaline lake will show reduced sensitivity to dust addition due to a lower nutrient release at higher pH levels. Third, we predict that dust enriched in P will enhance phytoplankton growth compared to dust richer in base cations (e.g., Ca^{2+}).

2. Material and methods

2.1. Experimental approach

Jordanelle Reservoir (40°36′27’’N, 111°24′50’’W; Utah) and Half-Moon Lake (42°55′30’’N, 109°44′15’’W; Wyoming) are aquatic

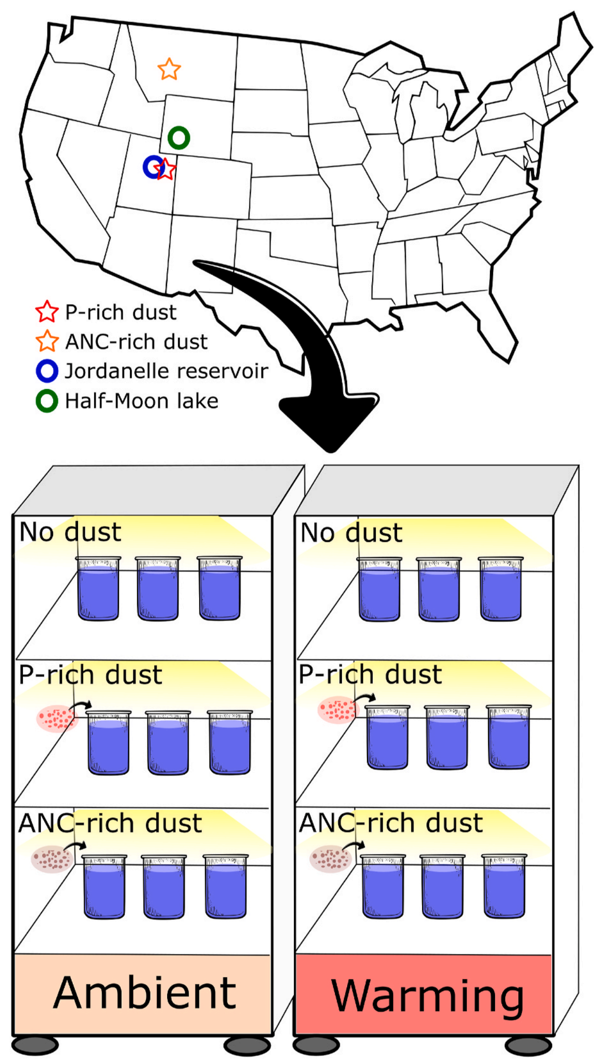

Fig. 1. Experimental design, including the geographic location of the aquatic ecosystems and the collected dust for our experiment. The experiment included two temperature treatments (Ambient and Warming) and three dust treatments (No dust, P-rich dust, and ANC-rich dust).

ecosystems situated in the western United States (see Fig. 1). Both ecosystems experience relatively high atmospheric dust deposition originating from arid and semi-arid regions in the western United States (Duniway et al., 2019). Additionally, the deposition of particles transported by wildfire smoke, associated with increasing human pressure in the western United States, also represents a significant input of particles to these ecosystems (Ball et al., 2021). Jordanelle Reservoir, located at an elevation of approximately 1880 m, serves as a water source for municipal, industrial, agricultural, wildlife, and recreational activities. Covering an area of 12.2 km^2 with a maximum depth of 85 m, it boasts a complex geological composition comprising alluvial deposits and materials associated with volcanic activity (Water and Environmental Resource division et al., 2012), where the weathering of carbonate and siliceous rocks occurs (Carling et al., 2015).

Half-Moon Lake, situated at an elevation of 2320 m, is a moraine lake with a total water surface area of 4.2 km^2 and a maximum depth of 86 m. Its basin is quartz-rich and highly insoluble, resulting in highly diluted water due to the shallow soil depth (Leopold, 1980). These ecosystems were chosen for study due to their similar trophic state (both being oligotrophic systems with low chlorophyll-*a* and total P values; see Table 1), making them highly sensitive to nutrient inputs. Additionally, they exhibit different physicochemical properties associated with the basin's characteristics, including differences in pH (neutral vs. alkaline), calcium levels (low vs. high), and dissolved organic carbon (high vs. low; see Table 1).

For our experiment, we collected 150 L water samples from each ecosystem using a 10 L Van Dorn bottle. Sampling took place at various discrete depths within the upper mixed layer on 5 and 25 July 2022 in Half-Moon Lake (mixing layer depth: 5.5 m) and Jordanelle Reservoir (mixing layer depth: 7.0 m), respectively. The water samples were then filtered through 80-μm Nitex mesh to remove zooplankton. Subsequently, they were transferred to a 200-L acid-washed opaque container and transported to the laboratory under darkness and temperature-controlled conditions.

2.2. Incubation conditions

Once in the laboratory, water samples were transferred into 10-L plastic microcosms and placed in two Conviron CMP6060 Environmental Chambers (Winnipeg, Manitoba, Canada), where they were kept in darkness and at the respective lake temperatures overnight before being used in the experiments. The following day (6th July 2022 for Half-Moon Lake and 26th July 2022 for Jordanelle Reservoir, hereafter referred to as the initial time), the experiment was initiated under the conditions described below. Microcosms were manually shaken every 4–5 h to prevent organisms from settling, ensuring they received homogeneous irradiance.

The experiment followed a split-plot design to investigate the effects of two global-change drivers: temperature (T) and dust (Dust), on plankton metabolism and composition. At the plot level, two temperature treatments were applied: ambient temperature (Amb) as the control and a warming treatment (W) with +5 °C. The ambient temperature was 15 °C in Half-Moon Lake and 22 °C in Jordanelle Reservoir. The 5 °C increase in temperature falls within the variation expected in global predictions for the late 21st century (IPCC et al., 2021; Scenario RCP8.5) and is consistent with the range of diel temperature variations observed in other freshwater ecosystems (Woolway et al., 2016).

Additionally, at the subplot level, there were six T × dust treatments: Amb, P-rich dust, ANC (Acid Neutralizing Capacity)-rich dust, W, W + P-rich dust, and W + ANC-rich dust. These treatments resulted from combining two temperature levels (ambient and warming) and three dust levels (No dust, P-rich dust, and ANC-rich dust; see Fig. 1).

In the first part of the experiment (main plot; from the initial time to day 5), microcosms from each system were maintained for 5 days exposed to approximately 120 μmol photons m^{-2} s^{-1} of cool white, fluorescent light under a 14:10 h light photoperiod, at the respective experimental temperatures (Ambient and Warming; 9 microcosms per temperature).

In the second part of the experiment (subplot; from day 6–10), environmental conditions in the chambers remained similar to the main plot, and dust treatments were amended with 50 mg L^{-1} of P-rich dust or ANC-rich dust. Although the amount of dust added in our experiment was very high, it corresponds to events of extreme intensity recently reported in the Euro-Atlantic area (Cuevas-Agulló et al., 2023). Furthermore, the amount of phosphorus released by our two types of dust ranged between 2 and 6 μg P L^{-1}, which falls within the values reported by Brahney et al. (2014) in alpine lakes in western Wyoming (USA) exposed to high dust deposition and is clearly lower than the 23 μg P L^{-1} reported by Villar-Argaiz et al. (2001) in Southern Europe.

2.3. Selection and preparation of dust

We used two types of dust with different compositions in our experiment to test how they affect the phytoplankton community: a) The P-rich dust was collected following a dust deposition event on the snow in Alta Mountain (Utah) in May 2022. In the western United States, dust deposited on snow in high mountain areas is also an important source of nutrients for aquatic ecosystems (Lang et al., 2023; Painter et al., 2010). Therefore, this approach allows us to obtain a more accurate representation of the different types of dust that can be deposited in the aquatic ecosystems of our study area. P-rich dust samples were obtained from the top 50 cm of the snowpack and pooled to create a single composite sample. To prevent potential leaching of nutrients from the dust, we extracted all the dust from the snow within 24 h. The snow samples were promptly transported to the laboratory, thawed and mostly evaporated at 50 °C. The remaining water containing dust was then centrifuged to separate the dust. Finally, the dust was dried at 50 °C in an oven to obtain dry dust. The total phosphorus results in the dust sample showed values of 0.6–0.8 mg P g^{-1} dust, similar to Scholz and Brahney (2022) and within the range of values obtained by Munroe et al. (2015) for dust samples collected in the Alpine regions of the Uinta and Wasatch Mountains in Utah. b) Additionally, we aimed to simulate mineral dust deposition using soil from other important sources such as agricultural areas. Cultivated drylands of the Great Plains region along with the arid and semi-arid western rangelands, comprises the most susceptible regions in the United States to wind erosion and soil loss (Hennen et al., 2022). For this purpose, we collected a soil sample from Clark (Montana,

Table 1

Initial values of light attenuation coefficient (K_d), mean PAR irradiance (I_m PAR), water temperature, pH, calcium concentration, total phosphorus (TP), total dissolved P (TDP), total dissolved N (TDN), dissolved organic carbon (DOC), sestonic N:P ratio, sestonic C:N ratio, Chl-*a* concentration, gross primary production (GPP), respiration (R), and GPP:R ratio in Half-Moon Lake and Jordanelle Reservoir. Significant differences (p-value from *t*-test analysis) between ecosystems are represented with asterisks: Single, double and triple asterisks denote a significant difference lower than 0.05, 0.01, and 0.001, respectively.

Variable	Half-Moon Lake	Jordanelle Reservoir	p-value
K_d PAR (m^{-1})	0.44 (0.03)	0.91 (0.04)	***
Water T (°C)	15 (0.2)	22 (0.3)	***
pH	7.29 (0.03)	8.12 (0.03)	***
Ca (mg L^{-1})	2.2 (0.1)	22 (1.1)	***
TP (μg L^{-1})	8.07 (0.98)	8.2 (1.03)	>0.05
TDP (μg L^{-1})	2.76 (0.36)	4.31 (0.91)	0.052
TDN (mg L^{-1})	0.24 (0.01)	0.24 (0.01)	>0.05
TDN:TDP ratio (molar)	192.5	123.3	
DOC (mg L^{-1})	2.95 (0.23)	4.83 (0.28)	***
Sestonic N:P ratio	15.35 (1.36)	15.13 (1.64)	>0.05
Sestonic C:N ratio	10.49 (0.21)	11.56 (0.38)	*
Chl-*a* (μg L^{-1})	0.91 (0.06)	1.58 (0.04)	***
GPP (μg C L^{-1} h^{-1})	10.5 (1.3)	5.1 (0.8)	**
R (μg C L^{-1} h^{-1})	2.3 (0.7)	4.5 (0.4)	**
GPP:R ratio	2.54 (0.18)	0.65 (0.04)	***

United States), characterized by its loamy sand texture and high calcium and magnesium content (hereafter referred to as ANC due to their high acid-neutralizing capacity in carbonates and hydroxide compounds). A dust analogue was generated from soil sieved through meshes with pore sizes up to 100 μm. Subsequently, the finest fraction was gently blown onto an inclined glass slide. The smallest particles retained on the slide (<10 μm) were collected using a brush (following Villar-Argaiz et al., 2018) and utilized as the ANC-rich dust in our experiment.

2.4. Characterization of the water column

For each ecosystem, we determine the vertical profiles of pH and temperature of water column at noon using a submersible multi-parametric probe (YSI Pro Plus, YSI Incorporated, OH, USA), and light using a submersible radiometer (Apogee's SQ-110 Original Quantum, USA) that registered measurements of downwelling irradiance at the full photosynthetic active radiation wavelength [400–700 nm]).

Diffuse attenuation coefficients for downward radiation (K_d) in the photic zone were determined from the slope of the linear regression of the natural logarithm of downwelling irradiance versus depth.

2.5. Remote sensing

Remote sensing data for the Half-Moon Lake and Jordanelle Reservoir areas were gathered from 1980 to 2022. To explore regional dust variations, monthly data on the area-average dust surface mass concentration for particulate matter <10 μm were downloaded from Giovanni v. 4.38. The data were sourced from the Modern-Era Retrospective Analysis for Research and Applications, Version 2 (MERRA-2), covering January 1980 to July 2022.

2.6. Chemical parameters

The pH and dissolved Ca in the water were measured during the incubation experiment (at the initial time, day 5, 6, 8, and 10) using 25 ml aliquots in a benchtop meter (SevenExcellence pH meter S400, Mettler Toledo), which includes a pH sensor and a combined ion-selective electrode for Ca (perfectION Comb Ca, Mettler Toledo).

The concentration of total phosphorus (TP) and total dissolved phosphorus (TDP) in water samples was determined in 15-ml aliquots after the addition of nitric acid (4.75 % w/w) in the Agilent 8900 Triple-Quadrupole ICP-MS. Total dissolved nitrogen (TDN) and dissolved organic carbon (DOC) samples were determined in 15-ml aliquots and measured in a TOC/TN analyzer (Skalar, Formacs^{HT-I} TOC/TN, The Netherlands). For the determination of dissolved nutrients, the water samples were previously filtered at low pressure (<100 mmHg) using glass-fiber filters (0.7 μm pore-size, Whatman GF/F).

To determine sestonic C, N, and P, water samples (0.25–0.5 L for C/N and 0.25–0.5 L for P) were filtered through pre-combusted (1 h at 550 °C) glass-fiber filters with a pore size of 0.7 μm (Whatman GF/F) at low pressure (<100 mm Hg). The filters were immediately frozen at −20 °C. Sestonic C and N analyses were performed using a Costech 4010 Elemental Analyzer. Sestonic P was determined after the filters were digested with a mixture of potassium persulfate and sulfuric acid at 120 °C for 30 min and analyzed as soluble reactive P using the acid molybdate technique (APHA, 1992).

The two types of dust (P-rich dust and ANC-rich dust) were chemically characterized to determine the presence and release of Na, Mg, Al, Si, P, S, K, Ca, Mn, and Fe from the dust into the water (see Table 2). The presence of these elements in the liquid fraction was analyzed by dissolving the dust in Milli-Q water for 24 h. Subsequently, 15-ml aliquots were diluted in nitric acid (4.75 % w/w) and measured using the Agilent 8900 Triple-Quadrupole ICP-MS.

2.7. Biological parameters

2.7.1. Chlorophyll-a concentration

Chl-*a* concentration was determined using the fluorometric technique. Samples were filtered onto a Whatman GF/F filter (0.7 μm pore size), and the photosynthetic pigments were extracted in 10 ml of absolute ethanol at 4 °C in darkness (Ritchie, 2008).

The samples were measured at an excitation wavelength of 436 nm and emission at 665 nm using a spectrofluorometer SpectraMax M2 reader (Molecular Devices, Sunnyvale, CA, USA). Prior to the measurements, a calibration curve was constructed using pure chlorophyll spinach extract to convert fluorescence values into chlorophyll concentration.

2.7.2. Primary production and respiration

During each sampling day and before the start of the light period, nine 60 mL Winkler flasks were filled for each treatment ensuring the prevention of bubble formation. Three flasks were used to measure the initial oxygen (O_2) concentration in the water, while the remaining six flasks (three clear and three dark) were incubated at their respective temperatures for 24 h (14 h light + 10 h dark). Following the incubation, Winkler reagents were added, and the flasks were sealed and kept in darkness for a maximum of 24 h before analysis (Carpenter, 1965).

Dissolved oxygen titration was performed using a 10 mL bottle-top burette (Titrette®, Brand GMBH, Germany; accuracy ±0.1 %) with colorimetric endpoint determination.

Net Community Production (NCP) was determined from the slope (positive or negative) of the oxygen concentration's evolution over 24 h in clear flasks, while community respiration (R) was determined from the negative slope of oxygen consumption over 24 h in dark flasks. Gross primary production (GPP) was calculated as the sum of NCP and R. Finally, oxygen values were converted to carbon values by multiplying by a conversion factor based on the photosynthesis reaction (i.e., 0.375).

2.7.3. Community composition

Cellular abundances and composition of the phytoplankton community at the initial time for each ecosystem and at the end of the experiment in each microcosm were determined using an imaging flow cytometer (Imaging FlowCytobot, McLane Research Laboratories, Inc.) from PhycoTech Laboratory (Michigan, United States). We filled 250-mL opaque plastic bottles with water from each ecosystem and treatment. The samples were then preserved by adding glutaraldehyde (0.25 % final concentration) and stored under cool, dark conditions until processing.

Simpson's diversity index, as a measurement of diversity, was calculated from abundance data as follows:

$$\text{Simpson's Diversity Index} = 1 - \sum (p_i)^2$$

where p_i is the proportion of individuals belonging to species i (Morris et al., 2014).

Table 2
Mean concentration of elements (in ppb) and their errors (in parentheses) released by 50 mg dust L^{-1} in Milli-Q® water.

Dust	Na	Mg	Al	Si	P	S	K	Ca	Mn	Fe
P-rich dust	22.8 (0.27)	3.32 (0.02)	1.02 (0.02)	6.67 (0.01)	2.31 (0.02)	1.87 (0.09)	2.50 (0.02)	12.8 (0.13)	0.17 (0.01)	0.97 (0.05)
ANC-rich dust	24.9 (0.35)	8.32 (0.18)	0.68 (0.06)	7.85 (0.17)	0.52 (0.01)	21.2 (0.39)	3.82 (0.05)	19.5 (0.54)	0.19 (0.01)	0.76 (0.06)

2.8. Numerical methods and statistical analysis

The gross primary production to respiration ratio (GPP:R) for accumulated values and for each treatment was calculated taking into account that GPP occurs during the light phase (14 h) and R occurs throughout the day (24 h).

To assess the magnitude and direction of the single effects of the studied factors, the effect size of temperature (Warming effect), and dust under ambient or warming conditions (P-rich dust effect, ANC-rich dust effect, P-rich dust effect under warming, and ANC-rich dust effect under warming) on the GPP:R ratio was calculated as follows:

$$\text{Effect size of warming }(\%) = \frac{\text{W} - \text{Amb}}{\text{Amb}} \times 100$$

$$\text{Effect size of P} - \text{rich dust }(\%) = \frac{\text{P rich dust} - \text{Amb}}{\text{Amb}} \times 100$$

$$\text{Effect size of ANC} - \text{rich dust }(\%) = \frac{\text{ANC rich dust} - \text{Amb}}{\text{Amb}} \times 100$$

$$\text{Effect size of P} - \text{rich dust under warming }(\%) = \frac{(\text{W} + \text{P rich dust}) - \text{W}}{\text{W}} \times 100$$

$$\text{Effect size of ANC} - \text{rich dust under warming }(\%) = \frac{(\text{W} + \text{ANC rich dust}) - \text{W}}{\text{W}} \times 100$$

A *t*-test analysis was conducted to determine the significant differences between the initial conditions of Half-Moon Lake and Jordanelle Reservoir.

The statistical significance of T as the main plot effect and T × Dust interaction as the subplot effect on each response variable (pH, Ca, TDP, TDN, DOC, sestonic N:P and C:N ratios, Chl-*a*, GPP, R) for each ecosystem over the experiment was assessed by a two-way split plot of repeated-measures analysis of variance (RM-ANOVA) after verifying the assumption of normality of residuals (by Shapiro–Wilk's test). The sphericity assumption was checked using Mauchly's test, and the Geisser-Greenhouse correction was applied when Mauchly's test indicated a violation of sphericity.

A two-way ANOVA was conducted to determine the statistical significances among treatments for each variable response (Accumulated GPP, accumulated R, GPP:R ratio, total cell abundance, phytoplanktonic functional groups abundance, and Simpson's diversity index) for each aquatic ecosystem.

To quantify the influence of biotic and abiotic factors (pH, Ca, total dissolved P, total dissolved N, dissolved organic carbon, sestonic C, sestonic N, sestonic P, C:N, C:P, and N:P ratios) on Chl-*a*, GPP, R, total cell abundance, and cyanobacteria abundances for both ecosystems, a step-forward multiple regression (SMR) was carried out. Linearity and multiorthogonality among independent variables were verified by previous correlation analysis, with a tolerance threshold of 0.6. The normal distribution of residuals in all regressions was checked by Kolmogorov-Smirnov tests.

3. Results

3.1. Remote sensing data of aerosols

Satellite data show a progressive increase in surface dust concentration for the two studied regions from 1980 to the present. Specifically, the slope showing dust concentration over time is slightly higher in the Jordanelle Reservoir area compared to the Half-Moon Lake area (0.0070 vs 0.0058, respectively; see Fig. 2). Additionally, the average concentration is also slightly higher in Jordanelle than in Half-Moon (5.83 vs 4.47 μg m^{-3}, respectively).

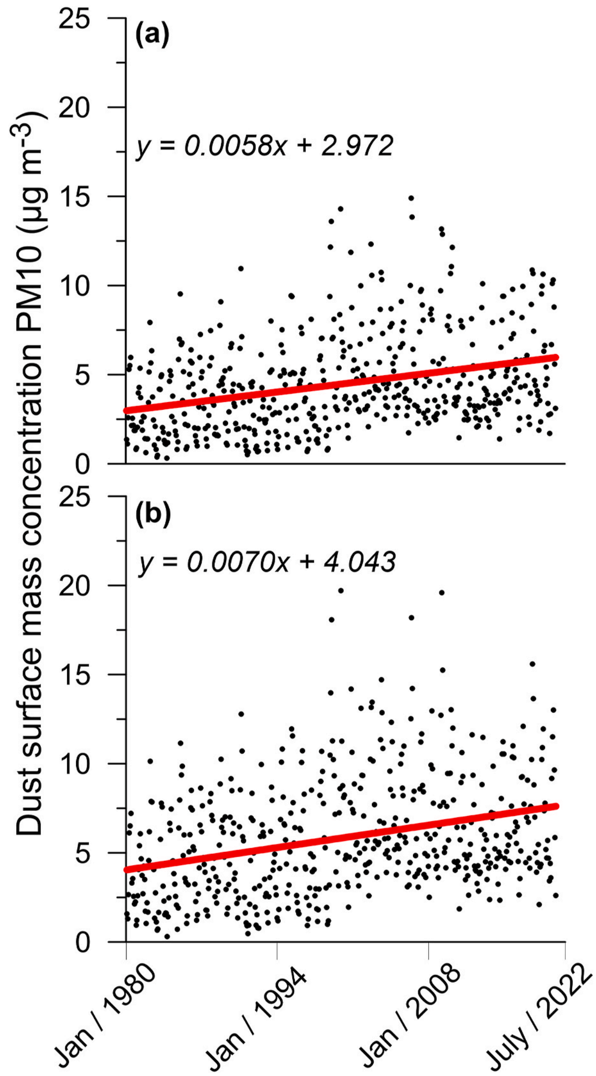

Fig. 2. Dust surface mass concentration for total particulate matter PM10 (in μg m^{-3}), for Half-Moon Lake (a) and Jordanelle Reservoir (b) areas during the period 1980–2022.

3.2. Initial and experimental physicochemical conditions

The studied ecosystems showed different physicochemical and biological properties at the beginning of the experiment (Table 1). Half-Moon Lake exhibited higher transparency ($K_d = 0.44$ m^{-1}) than Jordanelle Reservoir ($K_d = 0.91$ m^{-1}). Mean water T in the mixed layer, pH, Ca concentration, DOC, sestonic C:N ratio and Chl-*a* were lower in Half-Moon than in Jordanelle at the beginning of the experiment, whereas TP, TDP, TDN and sestonic N:P ratio were similar in both ecosystems (see Table 1). Half-Moon Lake showed higher GPP and lower R than Jordanelle Reservoir, which led the first ecosystem to exhibit a net autotrophic balance (GPP:R ratio >1), as opposed to the heterotrophic balance of the second (Table 1).

During the experiment, the addition of P-rich dust or ANC-rich dust increased pH and Ca levels in Half-Moon Lake, while in Jordanelle, no clear effect was observed (see Supplementary information, Figs. S1 and S2). TDP values increased following dust addition in both ecosystems and under both temperature conditions (Supplementary information, Fig. S3), while DOC values exhibited no significant variation (Supplementary information, Fig. S4). TDN values decreased in both Half-Moon and Jordanelle after dust addition, except under warming conditions in Jordanelle (Supplementary Information, Fig. S5).

In both ecosystems, the incorporation of P-rich dust (and ANC-rich dust in Jordanelle) yielded the lowest sestonic N:P ratio for both temperatures from day 6 until the end of the experiment (Supplementary information, Fig. S6). Regarding the sestonic C:N ratio, dust addition reduced the C:N ratio in Half-Moon and increased it in Jordanelle for both temperatures (Supplementary information, Fig. S7). Concerning Chl-*a* concentration, dust addition initially had a positive effect on Half-Moon until day 8, while at the final time only the treatments with dust at ambient temperature showed higher values. In Jordanelle, dust exerted a positive effect, resulting in an increase in Chl-*a* from day 8 (Supplementary information, Fig. S8).

3.3. Dust and warming effect on metabolism

The daily results of GPP and R for Half-Moon Lake and Jordanelle (see Supplementary Information Fig. S9) were represented as accumulated values to clarify the effects of the treatments (Fig. 3). Dust addition increased accumulated GPP and R in both systems, with a greater effect observed in P-rich dust treatment compared to ANC-rich dust treatment ($p < 0.05$, post hoc Fisher's LSD; except for accumulated R in Half-Moon Lake). The Warming treatment significantly increased accumulated R only in Half-Moon Lake ($p < 0.05$, post hoc Fisher's LSD; Supplementary Information Tables S3 and S4). Under the combined influence of warming and dust addition, GPP was enhanced by ANC-rich dust in Half-Moon Lake and by P-rich dust in Jordanelle Reservoir compared to ambient temperature conditions. As for accumulated R, values increased due to the Temperature × Dust interaction in both systems and for both dust types ($p < 0.05$, post hoc Fisher's LSD). Besides, the difference between dust treatments (P-rich vs ANC-rich dust) for each temperature was greater in Jordanelle ($p < 0.0001$) than in Half-Moon ($p < 0.05$), revealing a different magnitude of the effect of dust depending on ecosystem.

The GPP:R ratio calculated from the accumulated values indicates different trophic states for both aquatic systems under ambient conditions, with Half-Moon being autotrophic (GPP:R ratio >1) and Jordanelle being heterotrophic (GPP:R ratio <1; Fig. 4a). The analysis of effect size on GPP:R ratio shows a clear trend for both systems (Fig. 4b). Overall, in Half-Moon, dust pushed the system towards heterotrophy under both ambient and warming conditions (excluding P-rich dust in ambient conditions whose decrease was not significant). Conversely, the effect of dust in Jordanelle shifted the metabolic balance towards autotrophy for both temperature conditions. However, all interactive

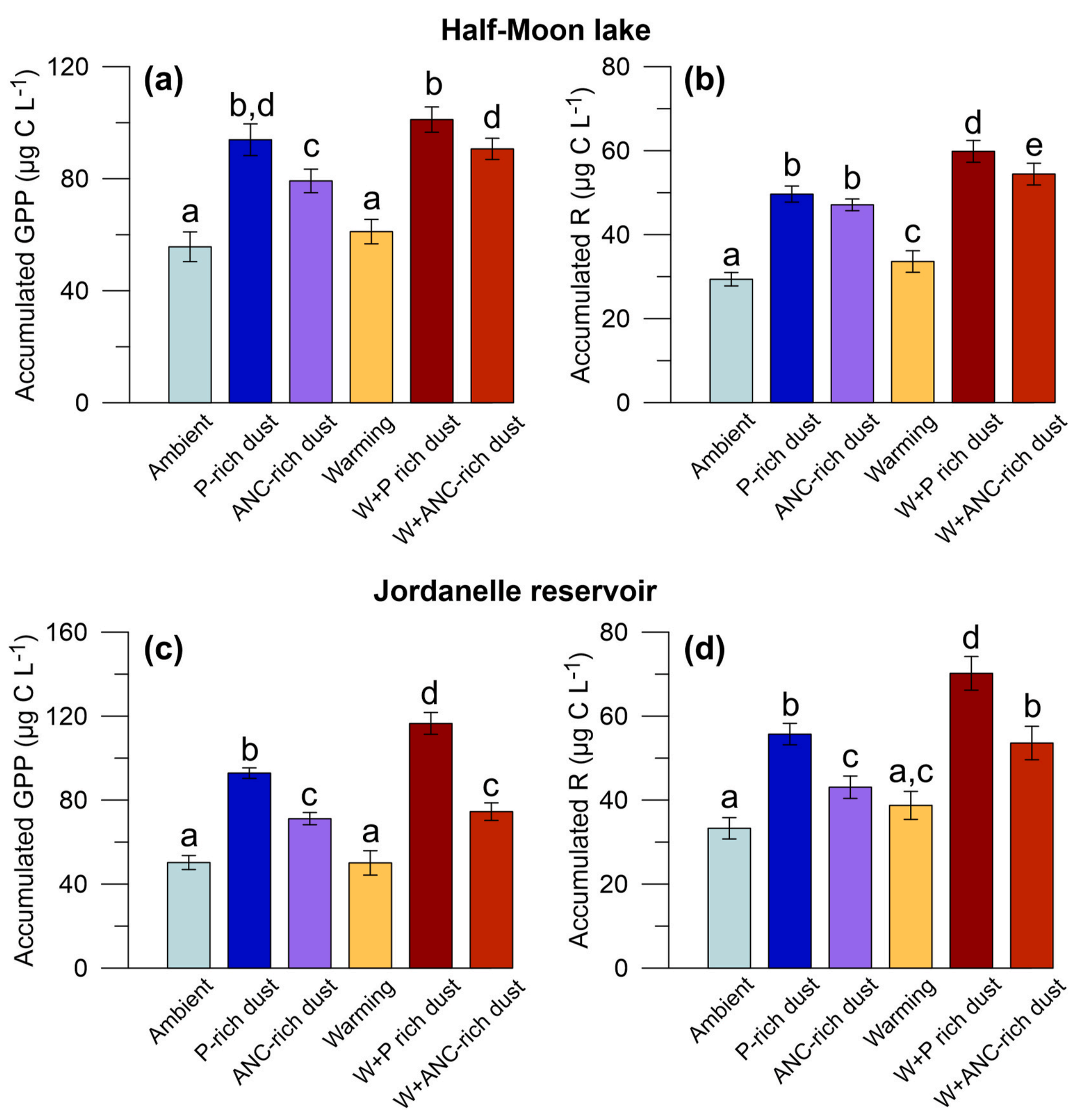

Fig. 3. Accumulated values of gross primary production (GPP) and respiration (R). Values are represented for the different treatments (Ambient, P-rich dust, ANC-rich dust, Warming, Warming + P-rich dust and Warming + ANC-rich dust) in Half-Moon lake (a,b) and Jordanelle Reservoir (c,d). The italic letters on the bars indicate differences among treatments. Data are expressed as mean values ± SD (n = 3).

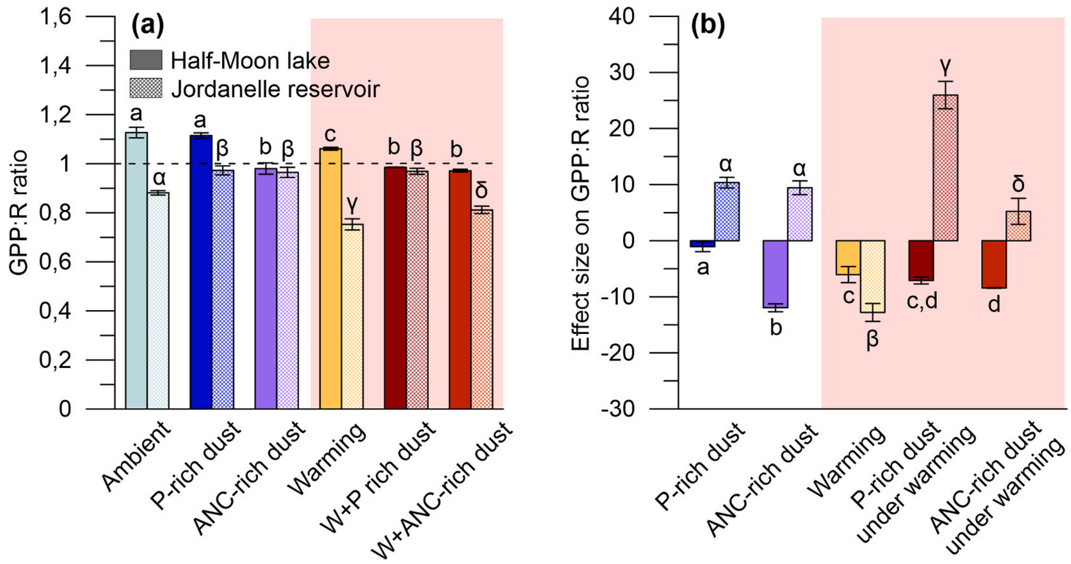

Fig. 4. a) Ratio gross primary production (GPP): respiration (R) for the accumulated values. Data are represented for the different ecosystems (Half-Moon Lake in solid bars, and Jordanelle Reservoir in striped bars) and treatments (Ambient, P-rich dust, ANC-rich dust, Warming, Warming + P-rich dust and Warming + ANC-rich dust). The horizontal line separates the autotrophic (>1) from heterotrophic (<1) metabolic balance, whereas the shaded area in red delineates the treatments exposed to warming conditions; b) Effect size of warming and dust treatments (P-rich and ANC-rich dust) under ambient and warming conditions. Positive values represent a stimulatory effect and negative values represent an inhibitory effect on GPP:R ratio. The italic letters on the bars indicate differences among Half-Moon Lake treatments, whereas the Greek letters indicate differences among Jordanelle Reservoir treatments. Data are expressed as mean values ± SD (n = 3).

treatments between warming and dust addition (i.e., W + P rich-dust and W + ANC-rich dust) in both systems showed a final heterotrophic balance (GPP:R ratio <1; Fig. 4a). Finally, the warming effect shifted the GPP:R ratio towards heterotrophy in both ecosystems (Fig. 4b).

The forward-stepwise multiple regression analysis revealed a positive correlation between GPP and the concentration of TDP, and between R and sestonic P in Half-Moon Lake, whereas in Jordanelle, GPP and R were negatively correlated with the sestonic C:P ratio and positively correlated with pH (see Table 3).

3.4. *Dust and warming effect on phytoplankton community*

The results show a highly significant impact of dust on increasing phytoplankton abundance in Half-Moon Lake, particularly cyanobacteria (Fig. 5a). This effect was more pronounced for treatments with ANC-rich dust compared to P-rich dust, under both thermal conditions ($p < 0.05$, post hoc Fisher's LSD; Supplementary Information Table S3). Notably, the growth of cyanobacteria in dust treatments significantly reduced the Simpson diversity index (Fig. 5c). The warming treatment did not stimulate cyanobacteria compared to the Ambient treatment. Instead, it promoted the growth of diatoms and chlorophytes, leading to an increase in the Simpson diversity index (Fig. 5c).

In Jordanelle, cellular abundance increased only in the treatment W + P-rich dust ($p < 0.05$, post hoc Fisher's LSD; Fig. 5b and Supplementary Information Table S4), primarily due to a significant effect on cyanobacterial abundance, which was six times higher than in the ambient treatment at the end of the experiment. Overall, both types of dust (P-rich and ANC-rich dust) promoted chlorophytes under both thermal conditions. Finally, the warming treatment had no effect on the abundance of functional groups compared to the Ambient treatment ($p > 0.05$, post hoc Fisher's LSD). In contrast to Half-Moon Lake, the addition of dust in Jordanelle did not have a widespread effect on reducing species diversity, or at least, it was not as pronounced (except for the W + P-rich dust treatment). In fact, the P-rich dust treatment showed higher diversity than the Ambient treatment ($p < 0.05$, post hoc Fisher's LSD; Fig. 5c).

The forward-stepwise multiple regression analysis showed that the abundance of cyanobacteria, mainly composed of individuals from the genus *Aphanocapsa*, was correlated with sestonic N and calcium in Half-Moon ($R^2 = 0.932$) and with sestonic P in Jordanelle ($R^2 = 0.648$; Table 3).

4. Discussion

Our study shows that the increasing intensity and frequency of dust storms, within the context of global warming, exert an effect on microbial structure and metabolism, which is primarily dependent on the biogeochemical properties of the watershed, and secondarily, on the

Table 3
Multiple stepwise regression for gross primary production (GPP), respiration (R) and cyanobacteria abundance in Half-Moon Lake and Jordanelle Reservoir (independent variables included in the table are only those which are statistically significant).

Dependent variable	Independent variable	n	Beta	Multiple R^2	R^2 exchange	*p* value
GPP – Half-Moon	TDP	19	0.748	0.534	0.534	<0.001
GPP – Jordanelle	C:P sestonic ratio	19	−0.689	0.314	0.314	0.012
	pH	19	0.452	0.188	0.502	0.026
R – Half-Moon	Sestonic P	19	0.517	0.298	0.298	0.016
	pH	19	0.452	0.501	0.203	0.021
R – Jordanelle	C:P sestonic ratio	19	−0.920	0.617	0.617	<0.001
	pH	19	0.472	0.822	0.205	<0.001
Cyanobacteria – Half-Moon	Sestonic N	7	0.618	0.761	0.761	0.010
	Calcium	7	0.485	0.932	0.171	0.034
Cyanobacteria – Jordanelle	Sestonic P	7	0.805	0.648	0.648	0.029

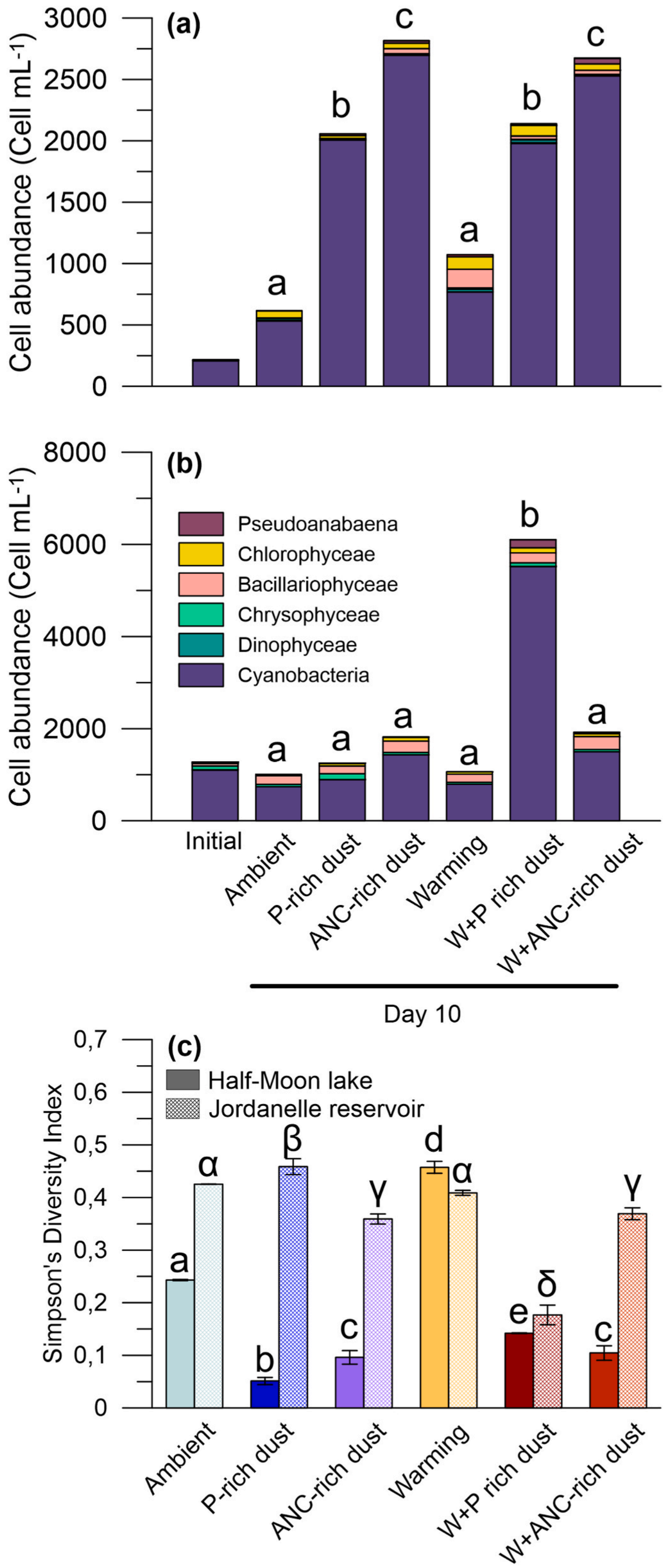

Fig. 5. Composition of the phytoplankton community. Values are expressed as cell abundance in Half-Moon lake (a) and Jordanelle Reservoir (b) at initial and final time, and Simpson's diversity index (c) for each of the treatments (Ambient, P-rich dust, ANC-rich dust, Warming, Warming + P-rich dust and Warming + ANC-rich dust). In panel (a) and (b), the italic letters on the bars indicate differences of total abundance among treatments. In panel (c), the italic letters on the bars indicate differences among Half-Moon Lake treatments, whereas the Greek letters indicate differences among Jordanelle Reservoir treatments. Data are expressed as mean values ± SD (n = 3).

composition of the dust. This important finding is discussed in detail under current and future warming conditions.

4.1. Dust effect under current temperature conditions

Firstly, our results indicate that under current temperature conditions, the addition of dust in Half-Moon Lake and Jordanelle Reservoir enhanced GPP and R. This effect was more pronounced for P-rich dust, likely because P was a limiting factor in both communities. Indeed, multiple regression analysis demonstrates the relationship between GPP and R with TDP and sestonic P in Half-Moon (positive relationship), and with sestonic C:P ratio in Jordanelle (negative relationship). Other elements present in the dust, such as iron (Fe), may have facilitated metabolic stimulation (see Sterner, 2008). Our chemical analysis shows that P-rich dust can release 17 nmol L^{-1} of Fe, significantly higher than the 13.6 nmol L^{-1} released by ANC-rich dust. Recently, Dengg et al. (2023) reported the critical role of Fe in regulating primary production and phytoplankton growth in New Zealand lakes when Fe concentrations exceed 0.8 nmol L^{-1}. These findings underscore the importance of dust as a highly nutritious mix of elements for planktonic organisms. Interestingly, while other dust sources have made a significant contribution of nitrogen to aquatic ecosystems (Wen, 2022), our results show that TDN did not increase after the addition of dust. Furthermore, regression analyses showed no relationship between N and metabolism (GPP and R).

Despite the stimulating effect of both dust types on the GPP and R of Half-Moon Lake and Jordanelle Reservoir, the metabolic balance (GPP: R) was strongly regulated by the biogeochemical properties of each ecosystem. Thus, the effect size of P-rich dust and ANC-rich dust on GPP: R showed negative values in Half-Moon Lake (trend towards heterotrophy) and positive values in Jordanelle Reservoir (trend towards autotrophy). The trend towards heterotrophy in Half-Moon Lake may be attributed to heterotrophic prokaryotes, which are particularly significant in oligotrophic ecosystems (Biddanda et al., 2001). These organisms exhibit a faster and more pronounced response to increased dissolved P availability due to their superior ability to capture nutrients under conditions of scarcity (Gazeau et al., 2021; Giovagnetti et al., 2013), thereby triggering bacterial respiration and decreasing the GPP:R ratio. On the other hand, a higher initial TDP concentration in Jordanelle, combined with the P contributions from dust, could support both the immediate demand by bacteria and the delayed demand by phytoplankton (Gazeau et al., 2021), thus supporting our results of an increased GPP:R ratio in this system. Therefore, the contrasting sensitivity of both communities in their metabolic variables to dust effects may be a consequence of their initial nutritional status (Romero et al., 2011; Winder, 2009).

The stimulatory effect of both dust types on the accumulated GPP of both ecosystems did not have the same impact on phytoplankton community structure. Only Half-Moon Lake showed a significant increase in cell abundance after dust addition, primarily driven by the growth of the cyanobacterium *Aphanocapsa* sp. This non-nitrogen-fixing cyanobacterium can store cyanophycin as a cellular nitrogen reserve (Allen et al., 1980). This ability could explain the observed correlation with sestonic N, and the reduction in TDN availability. It is important to emphasize that *Aphanocapsa* typically does not cause severe issues associated with blooms, but it is capable of producing toxic microcystins (Mioni et al., 2012). Therefore, monitoring is necessary to detect potential harmful blooms. Brahney et al. (2015a) and Zhang et al. (2021) reported, through limnological records, that the relative abundance of cyanobacteria in lakes of Western Wyoming (United States) and China, respectively, has increased in association with atmospheric dust deposition. Certain abilities of cyanobacteria, such as high-affinity phosphorus uptake in low-nutrient environments and the capacity to store and alternate between different nitrogen sources (Burford et al., 2023), likely enable them to outcompete their eukaryotic counterparts in Half-Moon Lake and other oligotrophic lakes (Sorichetti et al., 2014).

This competitive advantage can lead to bloom formation, contrary to the traditional understanding that blooms only occur in eutrophic ecosystems (Reinl et al., 2022). In Half-Moon Lake, the growth of cyanobacteria was primarily regulated by nitrogen and calcium. Traditionally, phosphorus has been recognized as the main limiting nutrient in the formation of cyanobacterial blooms, given the ability of many cyanobacteria to fix atmospheric nitrogen to meet their demands (Paerl et al., 2001; Smith, 1983). However, the increasing abundance of non-nitrogen-fixing cyanobacteria (e.g., *Aphanocapsa*) in lakes and reservoirs has led to a reconsideration of the importance of nitrogen in bloom formation in recent years (Harke et al., 2016). Additionally, Bonilla et al. (2023) reported that pH was positively correlated with cyanobacterial biomass in a study including 464 American lakes. In our findings from Half-Moon Lake, pH and calcium showed a high correlation, notably increasing in treatments with the addition of ANC-rich dust. Therefore, the increase in both parameters could be co-responsible for the greater abundance of cyanobacteria in ANC-rich dust treatments compared to P-rich dust treatments. Furthermore, ANC-rich dust contains a higher amount of sulfur, which could support the high growth rate of cyanobacteria since sulfur plays a pivotal role in the formation of structural and functional compounds such as amino acids, vitamins, cofactors, and cell wall constituents (Giordano and Prioretti, 2016). In this context, it is interesting to highlight the role of the nutrient mix in atmospheric dust, which increases the sensitivity of ecosystems to cyanobacterial growth. While other studies have reported that the critical total phosphorus threshold for controlling cyanobacterial growth ranges from 16 to 52 μg P L^{-1} in the Alpine and Northern European ecoregions (Poikane et al., 2022), from 10 to 100 μg P L^{-1} in Canadian lakes (Downing et al., 2001), and from 10 to 30 μg P L^{-1} in Finnish boreal lakes (Vuorio et al., 2020), in our study, cyanobacterial growth was detected at lower ranges (between 4.75 and 7 μg P L^{-1} in Half-Moon Lake). It is possible that the nutrient mix in the dust may interact, triggering community responses at lower absolute P concentrations than when P is added alone, highlighting the need for studies using realistic nutrient sources in ecosystems.

Regarding community structure in Jordanelle, the lesser effect of both dust types on cell abundance and diversity compared to Half-Moon may be attributed to the rapid depletion of nutrients after peaking on day 8, which subsequently limited the autotrophic response. In Jordanelle, only chlorophytes increased after the addition of both dust types, while chrysophytes increased only after the addition of P-rich dust. Similar results showing a minimal response of phytoplankton diversity to dust addition were reported by Giovagnetti et al. (2013). Additionally, the basin properties and its sensitivity to dust addition may have played an important role. A previous study by our group (González-Olalla et al., 2024) showed that lower pH can enhance nutrient availability for algal growth. Therefore, the lower pH of Half-Moon, associated with the siliceous composition of its basin, may have favored greater nutrient availability for growth. In Jordanelle, a higher pH may have limited nutrient release from the dust, thereby restricting cellular growth.

4.2. *Dust effect under future temperature conditions*

The 5 °C temperature increase, corresponding to the worst-case scenario projected by the (IPCC et al., 2021) for the year 2100, did not have a significant effect on the planktonic metabolism (GPP and R) of either lake, except for a slight increase in respiration in Half-Moon Lake. Similarly, the total abundance of phytoplankton and cyanobacteria did not increase under warming conditions. This lack of metabolic and structural response to warming in both lakes may be related to a limitation in the planktonic response under nutrient scarcity conditions (Marañón et al., 2018). Nevertheless, both ecosystems showed a trend towards a more heterotrophic metabolic balance, which aligns with predictions from the Metabolic Theory of Ecology (Brown et al., 2004).

The addition of dust after 5 days of acclimation to high temperatures produced effects in Half-Moon Lake comparable to those observed under ambient temperature conditions. Specifically, the addition of both dust types enhanced heterotrophy (GPP:R < 1) relative to the warming treatment. Furthermore, total phytoplankton abundance and cyanobacterial abundance were similar when dust was added under both warming and ambient temperature conditions. Regarding Jordanelle reservoir, under warming conditions, the community exhibited a trend towards autotrophy following the addition of both dust types, although GPP:R values remained below 1. Interestingly, only the W + P-rich dust treatment exhibited a significant increase in cyanobacterial abundance, suggesting that in this ecosystem, temperature played a more crucial role in cyanobacterial growth than in Half-Moon Lake. It is important to note that although some studies have predicted that the temperature threshold for triggering cyanobacterial proliferation is above 25 °C (Berg and Sutula, 2015; Paerl and Huisman, 2009) and the optimal temperature for a subspecies of *Aphanocapsa* is 35 °C (Allen et al., 1980), our results in Half-Moon Lake and Jordanelle Reservoir have shown that high cyanobacterial growth (and more specifically, *Aphanocapsa* sp.) can occur at lower ranges (15–27 °C), in line with other studies (e.g., 15–30 °C in Taihu Lake; see Yang et al., 2020). Despite this, results from both ecosystems indicate that the nutrients in the dust, rather than temperature, are the primary drivers in both systems. In fact, cyanobacteria growth in Jordanelle was mainly regulated by P (like Bonilla et al., 2023). Numerous studies have reported that nutrients are the primary factor, with temperature being a secondary one, in promoting higher cyanobacterial abundance in lakes across the United States (Ho and Michalak, 2020; Rigosi et al., 2014), Europe (Birk et al., 2020), and China (Zhang et al., 2021). It is interesting to analyze whether the potential interaction between nutrients and temperature (Paerl and Paul, 2012) could expand or alter the critical growth thresholds for cyanobacteria. Lürling et al. (2017) found that for an urban pond, an increase in temperature from 20 °C to 25 °C following a nutrient pulse resulted in a 174 % increase in cyanobacterial chlorophyll-a compared to ambient temperatures, and a further increase to 30 °C led to a 252 % increase. However, other studies have found no synergistic effects between both stressors when the temperature was increased from 20 to 25 °C in 39 urban water bodies (Lürling et al., 2018) or between 26 and 30 °C in Boqueirão de Parelhas reservoir (Brazil; see Souza et al., 2018). Rigosi et al. (2014) analyzed over 1000 lakes in the United States and reported that the interaction between temperature and nutrients on cyanobacteria was mostly additive, suggesting that extreme temperature could even lead to antagonistic interactive effects, similar to the results of Richardson et al. (2019). This variety of interactions aligns with our results, where we observed antagonistic effects in Half-Moon Lake for both types of dust, and a positive synergistic effect in Jordanelle Reservoir for the W + P-rich dust treatment. Therefore, it is important to consider the individual properties of each ecosystem when implementing management and ecological restoration tools in freshwater bodies. Our results suggest that the phosphorus concentration reduction proposed by other authors (Lehman et al., 2013; Schindler et al., 2016) may not be effective in controlling cyanobacterial growth, as other factors (temperature, interaction between nutrients transported by dust, prior nutritional status, and the biogeochemical properties of the ecosystem) can interact at low phosphorus levels, potentially even triggering blooms. Hence, an integrated approach to the ecosystem in question is required to understand the various mechanisms at play in the formation of such blooms.

5. Conclusions

This study reveals that atmospheric dust from various sources with differing composition can alter ecosystem metabolism and stimulate cyanobacterial growth. The metabolic and structural response of lake microbial communities is primarily shaped by the ecosystem's biogeochemical traits, while the chemical properties of the dust play a secondary role. The watershed sets the direction of the metabolic response, but the type of dust determines its intensity. Our findings suggest that lakes with lower pH may enhance nutrient release from the dust, driving significant metabolic shifts and changes in community composition, including potential cyanobacterial blooms. In contrast, lakes in calcareous basins (with higher pH) tend to limit nutrient release, reducing the dust's impact. In these cases, additional stressors, such as increased temperature, may be required to trigger noticeable changes in community composition. Then, the type of dust determines the magnitude of the change in metabolic balance and the increase in cyanobacteria in each ecosystem.

This work underscores how dust storms can induce cyanobacterial blooms and shows that the magnitude of this effect is governed by the biogeochemical properties of the receiving ecosystem. Therefore, an integrated approach to each ecosystem is necessary to establish the most appropriate management and restoration mechanisms.

CRediT authorship contribution statement

Juan Manuel González-Olalla: Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Janice Brahney:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization.

Funding sources

This study was supported by the National Science Foundation (2011910 and 1926559 to J.B.). J.M.G.-O. was supported by the National Science Foundation project 2011910 and 1926559.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Janice Brahney reports financial support was provided by National Science Foundation. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors are grateful to Daniela Aguirre and Camilla Moses for their help in the field sampling and sestonic nutrient analysis, and Dr. Karin Kettenring for letting us use the environmental chambers for the experiment.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envres.2025.121663.

Glossary

Amb	Ambient temperature treatment
ANC	Acid Neutralizing Capacity
Chl-*a*	Chlorophyll *a*
DOC	Dissolved Organic Carbon
GPP	Gross Primary Production
I_m	Mean Irradiance in the mixing layer
Kd	Mean attenuation coefficient
NCP	Net Community Production
R	Respiration
T	Temperature
TDN	Total Dissolved Nitrogen
TDP	Total Dissolved Phosphorus
TN	Total Nitrogen
TOC	Total Organic Carbon
TP	Total Phosphorus
W	Warming treatment

Data availability

The data that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.14795962, reference number 14795962.

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