Received: 26 June 2023 | Revised: 31 October 2023 | Accepted: 8 November 2023

DOI: 10.1111/gcb.17055

Global Change Biology WILEY

RESEARCH ARTICLE

Dust storms increase the tolerance of phytoplankton to thermal and pH changes

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Funding information
Division of Earth Sciences, Grant/Award Number: 2011910; Division of Environmental Biology, Grant/Award Number: 1926559

Abstract

Aquatic communities are increasingly subjected to multiple stressors through global change, including warming, pH shifts, and elevated nutrient concentrations. These stressors often surpass species tolerance range, leading to unpredictable consequences for aquatic communities and ecosystem functioning. Phytoplankton, as the foundation of the aquatic food web, play a crucial role in controlling water quality and the transfer of nutrients and energy to higher trophic levels. Despite the significance in understanding the effect of multiple stressors, further research is required to explore the combined impact of multiple stressors on phytoplankton. In this study, we used a combination of crossed experiment and mechanistic model to analyze the ecological and biogeochemical effects of global change on aquatic ecosystems and to forecast phytoplankton dynamics. We examined the effect of dust (0–75 mg L^{-1}), temperature (19–27°C), and pH (6.3–7.3) on the growth rate of the algal species *Scenedesmus obliquus*. Furthermore, we carried out a geospatial analysis to identify regions of the planet where aquatic systems could be most affected by atmospheric dust deposition. Our mechanistic model and our empirical data show that dust exerts a positive effect on phytoplankton growth rate, broadening its thermal and pH tolerance range. Finally, our geospatial analysis identifies several high-risk areas including the highlands of the Tibetan Plateau, western United States, South America, central and southern Africa, central Australia as well as the Mediterranean region where dust-induced changes are expected to have the greatest impacts. Overall, our study shows that increasing dust storms associated with a more arid climate and land degradation can reverse the negative effects of high temperatures and low pH on phytoplankton growth, affecting the biogeochemistry of aquatic ecosystems and their role in the cycles of the elements and tolerance to global change.

KEYWORDS
aerosol deposition, dust, growth rate, interactive effects, mechanistic model, pH, phytoplankton dynamic, temperature

1 | INTRODUCTION

Global change is leading to environmental conditions that exceed species tolerance ranges, resulting in unpredictable impacts on ecological communities and ecosystem functioning (Henson et al., 2021; Saavedra et al., 2013). As a result, there is a growing need to comprehensively assess the co-occurring environmental pressures at different levels of biological organization. However, few studies have targeted the effect of multiple stressors on population growth and fitness. Although understanding how individual factors influence population dynamics is vital, applying the findings to the actual world presents challenges (Orr et al., 2020). In the natural world, populations are concurrently affected by physical characteristics such as temperature and light, as well as biological factors such as predation, and chemical conditions including nutrient availability, pH, and others. These factors not only affect the dynamics of individual populations but also the communities in which they live (Kozik et al., 2019; Reynolds, 1984).

Understanding the impacts of multiple stressors is critical for primary producers, the organisms found at the base of trophic food webs. Phytoplankton, the primary producers in the pelagic zone of oceans and lakes, account for approximately half the global annual photoproduction and play a pivotal role in global biogeochemical cycles and the Earth's climate through the sequestration of carbon into freshwater and marine sediments (Falkowski et al., 2008; Mahowald et al., 2017) Production from phytoplankton is also disproportionately affected by human activities such as climate change, acidification, and pollution in both marine and freshwater environments, resulting in significant fluctuations in their growth conditions (Behrenfeld et al., 2006). Although numerous empirical studies have investigated the single and interactive effects of environmental factors and phytoplankton structure, ecology and/or physiology (e.g., Anderson et al., 2022; Elliott et al., 2006), performing experiments under multiple driving environmental conditions is necessary to develop tools for forecasting phytoplankton dynamics in a changing climate (Baird & Emsley, 1999; Thomas et al., 2017).

Nutrient availability and temperature are key environmental factors that control phytoplankton growth and they can act synergistically, stimulating algal growth (Fernández-González et al., 2022) by increasing metabolic, growth, and reproductive rates (Reinl et al., 2022). The growth curve of phytoplankton species and their responses to environmental nutrients can be represented by a saturation relationship (See Figure S1) that is theoretically described by Monod kinetics (Monod, 1949). Likewise, multiple studies have shown that temperature plays a crucial role in influencing chemical reaction rates, metabolism, and growth rate in ectothermic organisms, including phytoplankton. The temperature-controlled reaction rates conform to an exponential curve until they reach the optimum temperature (See Figure S1), a pattern shared from unicellular microbes to plants and animals (Gillooly et al., 2001). The effect of temperature on the growth of ectotherms follows an asymmetric curve characterized by unimodality and left skewness (Eppley, 1972; Kingsolver, 2009), which has biological and ecological implications as ectotherms are more sensitive to warming than cooling (Martin & Huey, 2008). In the context of global warming, this can lead to an increase in the risk of extinction for some species (Dillon et al., 2010). Some studies have shown that nutrients can influence the thermal tolerance curves of species, modifying the characteristics of the curve. Given that metabolic rates determine the rate at which resources are acquired from the environment and used for biological processes, it stands to reason that higher growth rates resulting from warming can only be sustained if sufficient nutrients are available. Maddux and Jones (1964) and Bestion et al. (2018) showed that the optimum growth temperature of some phytoplankton species, as well as their thermal range of growth, are higher or broader under high nutrient than under low nutrient conditions. However, these authors used chemical nutrients in their experiments, and thus it remains to be seen whether actual sources of nutrients associated with increasingly recurrent and intense events, such as atmospheric dust storms that are related to droughts and desertification (Javadian et al., 2019; Lambert et al., 2020), also have the ability to modify species tolerance ranges.

The role of global dust production in providing nutrients to the marine environment and resulting climate feedbacks on millennial timescales are well-established phenomena (Lambert et al., 2008). However, human activities and climate change have significantly increased the dust-mediated transport of nutrients to marine and freshwater environments, which has measurable impacts on seasonal, annual, and decadal timescales (Brahney et al., 2014; Brahney, Ballantyne, et al., 2015; Cabrerizo et al., 2016; Mladenov et al., 2011). Dust contains a variety of both macro- and micro-nutrients, the availability of which in freshwater environments is controlled by the source composition and changes during atmospheric transport, as well as conditions in the receiving environment, including pH and attendant nutrient limitation (Brahney et al., 2021; Stockdale et al., 2016). Modern dust derived from industrial, urban, combustion, and agricultural sources is likely to contain more phosphorus than historical dust, which has led to an approximate 40% increase in dust P deposition (Brahney, Mahowald, et al., 2015). In addition, studies have shown that low pH of atmospheric moisture can increase the solubilization of apatite mineral in dust, enhancing the bioavailability of *P* (Baker et al., 2021; Nenes et al., 2011). However, acidification can affect the acid base balance in phytoplankton and the efficacy of phosphatase enzymes (Flynn et al., 2012; Rost et al., 2003), which can lead to reduced primary production and growth (Gerloff-Elias et al., 2005). Hinga (2002) and Hansen (2002) reported that the growth rate of phytoplankton generally had a unimodal relationship with pH values (See Figure S1), with the optimal pH being species dependent. Therefore, studying how ecosystem pH affects nutrient release from dust at different temperatures and their interactive impact on phytoplankton functional traits represents a novel approach.

Because of the complex factors that affect the dynamics of phytoplankton populations, mechanistic models are a particularly useful tool for analyzing the ecological and biogeochemical effects of global change on aquatic ecosystems (Longhurst et al., 1995; Medvinsky et al., 2019). These models, combined with empirical data, can be used to forecast phytoplankton dynamics. Here, we develop a semi-empirical model explaining the role of pH affecting the nutrient release from dust and a mechanistic model that incorporates the effect of dust, temperature, and pH on the growth rate of a phytoplanktonic species (*Scenedesmus obliquus*). We use a common freshwater algal species and fit a tolerance function that is dependent on these three factors. We decided to work with a freshwater model species, given that these ecosystems are particularly vulnerable to global change, including the effects of dust, warming, and spatio-temporal variations of pH (Woodward et al., 2009, 2010). Our aim is to present an individual mechanistic model that builds upon previous models (e.g., Briere et al., 1999; Monod, 1949; Thomas et al., 2017) and to test it empirically. This represents a critical step in understanding the impacts of multiple environmental stressors, including realistic sources of nutrients, in the analysis of global change on the growth of a model species of freshwater phytoplankton.

1.1 | Model description

Our model of population growth for phytoplankton is based on the nutrient availability (measured as phosphorus, [P]) released by dust, temperature, and pH. First, using experimental data, we build a novel semi-empirical model that allows us to describe the release of *P* from dust at different pH and temperatures (Nutrient model), assuming that *P* is the main limiting nutrient in our phytoplankton population and will have a greater effect on population growth. Next, we introduce a mechanistic model of population growth for phytoplankton (Growth model) based on the availability of phosphorus obtained in the Nutrient model, temperature, and pH. Both models are described in detail below.

1.1.1 | Nutrient model

Our semi-empirical model predicts the concentration of nutrients (phosphorus) in the environment based on theoretical considerations, with experimentally determined constants (see Table S1). We establish that final *P* concentration depends on initial *P* concentration (P_0, in μg L^{-1}), dust concentration added to the medium (*Du*, in mg L^{-1}), pH, and temperature (*T*, in °C).

Assuming that final *P* is the result of the equilibrium of a chemical reaction,

$$P = P_0 + \frac{k_1}{k_2} Du, \quad (1)$$

where k_1 and k_2 are the forward and backward rate constants of the reaction. We also assume that the balance between forward and backward rates is sigmoidal with the exponent depending directly on pH and is sensitive to temperature via an Arrhenius function, as follows:

$$P = P_0 + \alpha \frac{Du}{1 + \exp\left(\beta_1 + \beta_2 pH - \frac{\beta_3}{T+273}\right)}, \quad (2)$$

where α is the maximum yield of *P* from dust, β_1 is a parameter controlling the location of the inflection point at nominal pH and temperature, β_2 captures the sensitivity to pH, and β_3 is proportional to the activation energy in the Arrhenius model (see values of parameters in Table S1). This model is fitted to the available phosphorus in our experiment 24 h after dust addition ($R^2 = .903$; see Figure 1a,b).

1.1.2 | Growth model

The net population growth rate (μ) can be described as the difference between the cell division rate and the death rate in the population (similar to Thomas et al., 2017). We assume that growth (*g*) is positively controlled by: (a) increasing temperature (*T*) until reaching the optimum; (b) availability of nutrients released by dust follows a saturation curve; and (c) optimal pH range follows a unimodal curve. The death rate (*d*) in the population is controlled by: (a) supra-optimal temperature; and (b) pH above or below the optimum:

$$\mu = g\,(T, Du, pH) - d\,(T, pH). \quad (3)$$

We describe the control of nutrients on growth (*g*) through the Monod equation:

$$g = b(T) \times \frac{P}{P+K}, \quad (4)$$

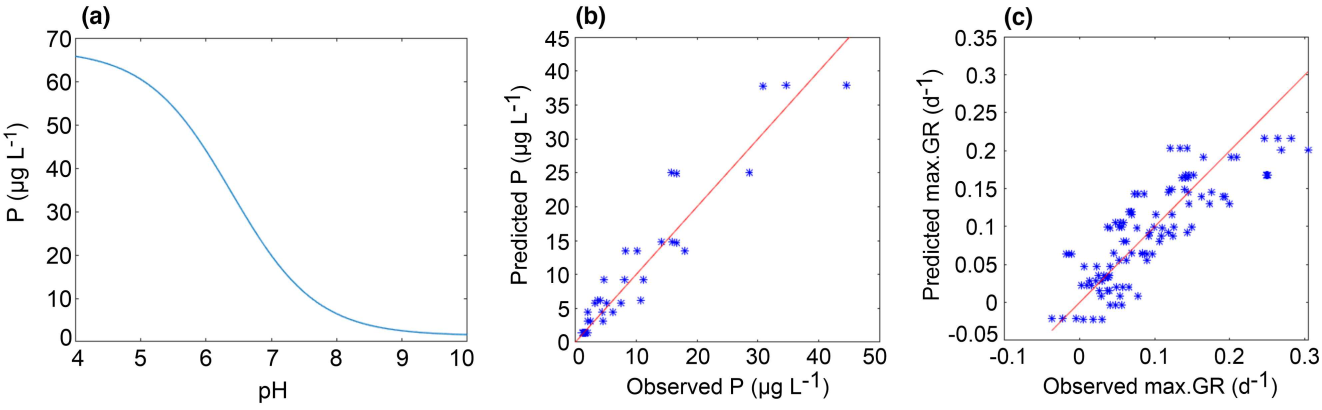

FIGURE 1 (a) Nutrient model prediction for phosphorus released from dust (μg P L^{-1}) at different pH and 20°C; (b) Predicted versus observed available phosphorus (μg P L^{-1}) after 24 h of dust addition ($R^2 = .903$) under three temperature levels (19, 23, and 27°C), three pH levels (6.3, 6.8, and 7.3) and four dust concentrations (0, 10, 25, and 75 mg L^{-1}). Note that the plot of predictions against observations illustrates the growth of variance with predicted phosphorus, consistent with the multiplicative log-normal model for observational variance; (c) Predicted versus observed maximum growth rate ($R^2 = .691$) under three temperature levels (19, 23, and 27°C), three pH levels (6.3, 6.8, and 7.3) and four dust concentrations (0, 10, 25, and 75 mg L^{-1}).

where $b(T)$ is a thermal rate function, P is the available phosphorus concentration according to Equation 2, and K is the half-saturation constant for uptake of phosphorus that depends on temperature and pH,

$$K = c_1 \exp\left[c_2\,(\Delta \mathrm{pH}) + c_3(\Delta \mathrm{T})\right], \tag{5}$$

where c_1 is the half-saturation value in nominal conditions and the other two c_j reflect the unknown sensitivity of the half-saturation value to pH and temperature (see values in Table S2). ΔpH and ΔT represent the variation in pH and temperature with respect to the optimal pH (pH-7.3) and temperature (T-23) for our species, respectively.

For the thermal rate function we follow the temperature-dependent model for ectotherms proposed by Briere et al. (1999),

$$b(T) = aT \times \left(T - T_{\mathrm{b}}\right)\sqrt{T_{\mathrm{m}} - T} \text{ and } b(t) = 0 \text{ if } T < Tb \text{ or } T > Tm, \tag{6}$$

where T_{b} and T_{m} are lower and upper thresholds, respectively. To make the curve more stable during estimation we rescale following (Wangen, 2021), and introduce nutrient dependence to the upper threshold. This gives

$$b(T,P) = b_1 T \times \left(T - T_{\mathrm{b}}\right)\sqrt{1 - \frac{T}{\left(b_2 + b_3 P\right)}} \tag{7}$$

where b_1 is the change in the reproduction rate with increasing temperature, b_2 is the base upper threshold for T_{m}, and b_3 is the nutrient increase rate for T_{m}.

Finally, we assume that death rate increases exponentially with temperature, and we also include the possibility that death rates may increase with pH deviation from optimal, giving

$$d(T, pH) = d_0 + d_1 \exp\left[-d_2(\Delta \mathrm{pH})^2 + d_3(\Delta T)\right]. \tag{8}$$

Here d_0 is the baseline of mortality rate across environmental conditions, d_1 is the additional rate of mortality away from nominal conditions, and d_2 and d_3 reflect the acceleration of death rate due to suboptimal pH and temperature, respectively.

The growth model is fit to the growth rate data from our experiment ($R^2 = .691$; see Figure 1c) and the result of the Growth model is represented in Figure 2.

2 | MATERIALS AND METHODS

2.1 | Culture conditions

The ubiquitous phytoplanktonic species *Scenedesmus obliquus* was obtained from the University of Texas-UTEX Culture Collection of Algae. We chose this species due to its wide geographical distribution, including oligo-meso-eutrophic systems (Johnson et al., 2007; Naumann, 1927; Sánchez-Castillo, 1988; Talib et al., 2008; Tas & Gonulol, 2007; Tolotti, 2001), fresh and brackish waters (An et al., 1999; Redden & Rukminasari, 2008), and its ecologically significant role, constituting a significant portion of the biomass of phytoplanktonic green algae (Van Vuuren et al., 2006; Yuan et al., 2023). It was cultured under non-axenic conditions in diluted Bold's Basal Medium (BBM), with a limited P supply and a concentration of approximately 2 μg P L^{-1}. *S. obliquus* was cultured in a Conviron CMP6060 Environmental Chamber (Winnipeg, Manitoba, Canada) under a regulated temperature of 19°C. It was exposed to ca. 120 μmol photon $\mathrm{m}^{-2}\,\mathrm{s}^{-1}$ of a cool white fluorescent light under a 12:12 h photoperiod.

Prior to the experiment, *S. obliquus* was acclimated to three temperature treatments [low (19°C), medium (23°C), and high (27°C) temperature] in environmental chambers and three pH levels (6.3, 6.8, and 7.3), for at least five generations. The pH was

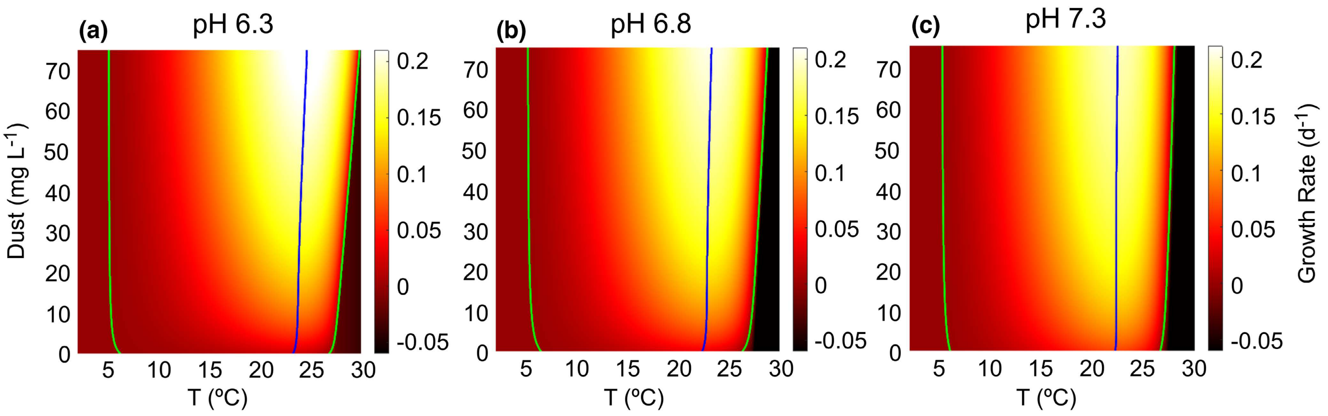

FIGURE 2 Growth rate (day^{-1}) model for *Scenedesmus obliquus* under a gradient of dust (mg L^{-1}), temperature (°C), and pH 6.3 (a), 6.8 (b), and 7.3 (c). Dust concentrations are showed in the left *y*-axis, growth rate values in the right *y*-axis, and temperature values in the *x*-axis. Green lines represent the limits for thermal tolerance of phytoplankton, whereas the blue line represent the optimum temperature for phytoplankton growth. Please note that the growth rate is indicated by the color gradient, which increases toward the upper right corner of the box, shown in yellow-white.

maintained constant using 0.5 M piperazine-N,N′-bis(2-ethanesulfonic acid) (PIPES) buffer in order to prevent pH changes after the addition of dust that could hinder the interpretation of the results. Both temperatures and pH are in the range of *S. obliquus* growth (Difusa et al., 2015; Zhang et al., 2019). During this phase, cell cultures were grown semicontinuously in diluted BBM in 4-L flasks and maintained at a mean cell abundance of approximately 7.5×10^4 cell mL^{-1}.

2.2 | Experimental set up

For the experiment, we aimed to assess the impact of different levels of dust concentration on phytoplankton growth across various combinations of temperature and pH. To achieve this, we established 36 treatments consisting of three different temperatures, three pH levels, and four different dust concentration levels (0, 10, 25, and 75 mg dust L^{-1}), each repeated in triplicate. Samples from 4-L flasks were distributed in one hundred and eight Erlenmeyer flasks of 250 mL each (36 replicates per temperature and pH and 27 replicates per dust concentration) that were acid-washed before the inoculation of the samples. Thirty-six flasks for each temperature were incubated in their respective environmental chambers. Then, we added dust to each Erlenmeyer flask separately and they were incubated for 7 days at the same conditions of pH and temperature of the acclimation phase. The flasks were shaken twice a day, before the cell abundance measurement and at noon, in order to prevent the sedimentation of *Scenedesmus* cells.

2.3 | Dust collection

Atmospheric deposition samples were collected from five dry sampling units (DSUs; see Brahney et al., 2020) located across the western United States in collaboration with the National Atmospheric Deposition Program (NADP). The DSUs are able to recover up to 97% of the gravitational dry deposition that enters the sampler (Brahney et al., 2020). To obtain a representative sample of dust deposited over the western United States, dust samples were pooled from five locations including Arizona, California, New Mexico, Idaho, and Texas (Table S3). The dust used was collected over the spring and summer months of 2021. The amount of dust from each station that was part of the final dust mixture was proportional to the amount of dust deposited in each collector. Thus, the dust collected at the Arizona station in the summer and the Texas station in the spring represented up to 40% of the composition of the dust used in our experiment (see Table S3). Since a wide range of dust and phosphorus concentrations is necessary to characterize the phytoplankton response to current and foreseeable future dust inputs, we decided to establish a range from 0 to a maximum concentration of 75 mg dust L^{-1}, corresponding to an event of extreme deposition like the one occurred in the Western Mediterranean and Euro Atlantic region during the winter–spring of 2022 (Cuevas-Agulló et al., 2023). In a previous experiment, this high amount of dust released from 15 to 40 µg P L^{-1}, depending on water pH. Nevertheless, the release of *P* into the environment during actual dust deposition events has been observed within the range of our previous experiment. For instance, Villar-Argaiz et al. (2001) reported an increase in *P* concentration in Laguna de La Caldera (South Spain) of 23.23 µg P L^{-1} after an external loading event in 1996. Additionally, Brahney et al. (2014), reported higher *P* concentrations (7–12 µg P L^{-1}) in alpine lakes in western Wyoming (USA), exposed to only moderate dust deposition rates compared to nearby lakes with little to no atmospheric deposition. Therefore, the *P* released by the dust falls within the range of previous and potentially expected *P* inputs into the aquatic environment following an atmospheric deposition event.

2.4 | Growth rate

Throughout the 7 days of the experiment, we measured the cell abundance for each of the replicates daily, using a 3.5 mL subsample. Subsamples were put into a quartz cuvette and the cell abundance was measured via chlorophyll *a* fluorescence at 436 and 680 nm of excitation and emission wavelength, respectively, in a SpectraMax M2 reader (Molecular Devices, Sunnyvale, CA, USA). Growth rate (μ) was calculated from cell abundance as follows:

$$\mu = \frac{\ln(C_2) - \ln(C_1)}{t_2 - t_1}$$

where C_j is the cell abundance (cell mL^{-1}) at times t_2 and t_1. Since some of the treatments reached the peak of cell abundance before others, we used the maximum growth rate calculated throughout the 7 days for each treatment.

2.5 | P cell quota

Subsamples of 15 mL of each flask were filtered at low pressure through precombusted (1 h at 550°C) glass-fiber filters of 0.7 µm pore size (Whatman GF/F; Whatman®, Sanford, ME, USA). Because nutrient uptake, and consequently cell quota, fluctuate throughout the growth phase of phytoplankton, we measured the *P* cell quota in each *Scenedesmus* culture at the point of peak abundance. Filters were immediately frozen at −20°C. Elemental *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* by applying the acid molybdate technique (APHA, 1992).

2.6 | Soluble reactive phosphorus (SRP)

After 24 h of dust addition, 25 mL subsamples of the culture were filtered using the same procedure as for *P* cell quota. The soluble reactive phosphorus (SRP) concentration in the filtrate was measured on a Lachat QuikChem 8500 Flow Injection analyzer. The method is based on phosphomolybdenum blue method (Murphy, & Riley, 1962).

2.7 | Spatial analysis

We carried out a geospatial data analysis in order to detect the continental regions of the planet that will be more affected by atmospheric dust deposition. First, we displayed the planet's soils according to their pH (acidic <7, neutral = 7, basic >7) and their cation exchange capacity (CEC; low, 0–15 meq/100 g; medium, 16–25 meq/100 g; high >26 meq/100 g) based on data obtained from the Harmonized World Soil Database (version 1.2). We assume that freshwater pH will be related to soil and bedrock pH as well as its CEC. Thus, regions with acidic pH and low CEC will be the most sensitive. We also differentiate between regions with similar pH but different CEC because where the CEC is lower (and, therefore, its capacity to neutralize acids is lower), the environment will be more sensitive to dust inputs. Next, these spatial data were combined with the projections of global temperature increase over the 21st century according to the RCP6.0 scenario (IPCC, 2021). As a result, we represent a map showing those areas of the planet that are sensitive to dust impact. Those areas with low pH and CEC, and high temperature increase, are highly sensitive. Contrarily, those areas with basic pH and high CEC, and lower temperature increases, are the least sensitive.

Spatial data for areas potentially sensitive to dust deposition (only those with medium sensitivity or higher) were combined with dust deposition data worldwide ($\text{g m}^{-2}\text{year}^{-1}$), obtained from Kok et al. (2021). We have taken into account the natural sources of dust over the world, since they are the most important source of atmospheric *P*, supplying about 83% of the total global sources of atmospheric *P* (Mahowald et al., 2008). Finally, we carried out an intersection geospatial analysis for displaying the regions of the planet according to the level of impact of dust, taking into account the soil properties, the foreseeable impact of temperature and atmospheric dust deposition from natural sources. The spatial data analysis was carried out using the QGIS software, Quantum Geographic Information System (version 3.16.15-Hannover, 2020).

2.8 | Statistical analysis

2.8.1 | Nutrient and growth model

We applied maximum likelihood to fit our nutrient model to the SRP values obtained in our experiment to determine the parameters of our model (see Table S1). We tested three experimental variance models and obtained the best results when the error was assumed to be multiplicative with log-normal distribution. We utilized the fitted nutrient model to predict available phosphorus levels for each of the 36 treatments (3 temperature × 3 pH × 4 dust treatments). Variance was assumed to be additive with a normal distribution. To eliminate spurious parameter estimates and regularize the error surface, weakly informative priors were multiplied by negative log likelihood. The growth model's parameters were determined using maximum posterior likelihood, which involved computationally minimizing the negative log posterior likelihood (see Table S2).

2.8.2 | Experimental data

The effect of temperature, pH, dust, and their interaction on all response variables of our experiment (growth rate, SRP, and *P* cell quota) was tested using a factorial analysis of variance (ANOVA). The assumption of normality was verified by the Kolmogorov–Smirnov test and data were logarithmically transformed when assumptions were not satisfied. The differences among treatments were assessed by the post hoc Fisher's least significant difference (LSD) test when significant interactive effects were found. The analyses were performed with the STATISTICA v7.0 software.

The data and model code that support the findings of this study are openly available (González-Olalla et al., 2023; https://doi.org/10.5281/zenodo.10081892).

3 | RESULTS

3.1 | Model results

The growth model shows that under conditions of no dust addition and phosphorus limitation, low pH (6.3) has a negative effect on phytoplankton growth compared to higher pH (6.8 and 7.3; Figure 2; Figure S2). The lowest pH shows a maximum growth rate of 0.021 days^{-1} under no dust addition, whereas at 6.8 and 7.3 the maximum growth rate is 0.034 and 0.067 days^{-1}, respectively (Table S4). Optimum temperature (22.1–22.9°C) and thermal tolerance range are similar for the three pH levels under no dust addition. However, our model shows that as the dust concentration increases: (a) the maximum growth of *S. obliquus* increases from values ranging 0.021–0.067 days^{-1} under no dust addition to 0.192–0.223 days^{-1} in treatments with 75 mg dust L^{-1}; (b) the thermal tolerance range widens for all pH values, being this greater at pH 6.3 due to a higher phosphorus availability. Thus, the combination of low pH and high dust concentration (75 mg L^{-1}) results in the widest range of thermal tolerance and growth rate for *S. obliquus*, so the thermal range increased from an upper thermal limit of 27°C under no dust addition to 30°C under highest dust addition and lowest pH; (c) the negative effect of low pH at low dust concentrations shifts to a positive effect at high dust concentrations and high temperatures; (d) the optimum temperature progressively increases with dust addition, from similar values for all the pH treatments under no dust addition to a maximum optimum temperature (24.7°C) under 75 mg dust L^{-1} addition and pH 6.3 (see Figure 2; Figure S2 and Table S4).

3.2 | Experimental results

The addition of dust led to a progressive increase in the soluble reactive phosphorous (SRP) concentration for all the temperature and pH treatments (Figure 3 and Table S5; $p < .05$). Furthermore, there is a trend toward a greater SRP availability when the pH drops from 7.3 to 6.3 for each temperature treatment (Figure 3). Consequently, the average SRP values after the addition of 75 mg dust L^{-1} ranged from 14 to 17 μg P L^{-1} at pH 7.3 to 30–45 μg P L^{-1} at pH 6.3. These results align with the pattern expected from our nutrient model. As a result, our predicted phosphorous concentrations in our nutrient model fit well to our SRP results at three temperatures, three pH, and four dust conditions ($R^2 = .903$; Figure 1b).

The growth rate of *S. obliquus* was stimulated by an increase in dust for all temperature and pH treatments (Figure 4 and Table S5; $p < .05$). In regard to the effect of temperature, our analysis of variance shows that there is a slight stimulation in the growth rate of *S. obliquus* from 19 to 23°C. However, the treatments at 27°C exert an overall negative impact on the growth rate ($p < .05$; Table S5). Furthermore *S. obliquus* exhibited a higher growth rate at pH of 6.3 and 7.3 than at pH 6.8 ($p < .05$; Table S5). As result of these single factor effects, we observed a shift in the response pattern. Thus, at low temperatures, there is a positive effect of high pH (7.3) on the growth rate compared to lower pH (6.8 and 6.3). As temperature increases, this pattern shifts toward a higher growth rate when pH decreases to 6.3 (Figure 4). In this way, growth rate values are higher at pH 6.3 when temperature reaches 27°C. Moreover, our results show that negative effect of high temperature on growth rate is reverted when high dust concentration (≥25 mg L^{-1}) is added under low pH (6.3; Figure 4). The growth rate data from our experiment are fit to our growth model ($R^2 = .691$; see Figure 1c).

The phosphorus cell quotas ranged from approximately 500 fg *P* $cell^{-1}$ to ca. 2400 fg *P* $cell^{-1}$ (see Figure 5). Overall, the results demonstrated a significant increase in *P* cell quota with higher dust additions, except for a few treatments with 25 or 75 mg dust L^{-1}. Similar to the growth rate pattern, *P* cell quota increases with higher pH under the low-temperature treatment (19°C), whereas this pattern is reversed at high temperature (27°C) with higher *P* cell quota observed under lower pH (Figure 5). Moreover, the treatments with high temperatures (27°C) and low pH (6.3) lead to higher *P* cell quota in *S. obliquus* after dust addition (Figure 5).

3.3 | Global impact of dust depending on soil sensitivity and warming

Our geospatial analysis predicts the impact of atmospheric dust deposition on inland aquatic ecosystems (Figure 6). Based on global dust deposition rates (Figure 6a; see Figure S3 for more detail) and the potential sensitivity of soils to dust deposition (Figure 6b, see Figures S4 and S5 for more detail) some areas in the western United States, South America, central and southern Africa and Asia, central Australia as well as the Mediterranean region will be highly or very highly impacted by dust deposition (Figure 6c; see Figure S6 for more detail of each continent). These areas are characterized by high dust deposition, soils very sensitive with pH ≤6.5 or low cation exchange capacity, and the forecast of a high temperature increase compared to other areas. Some areas with sensitive aquatic systems that are expected to experience strong temperature increases were not determined to

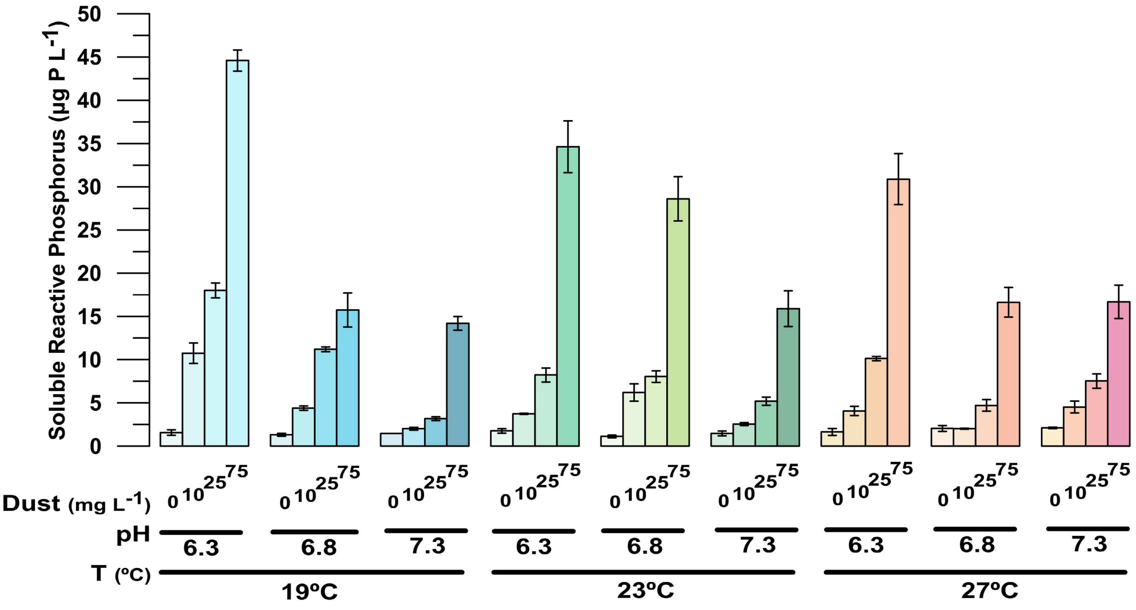

FIGURE 3 Soluble reactive phosphorus (SRP, μg P L^{-1}) after 24 h of dust addition under different treatments of temperature (19, 23, and 27°C), pH (6.3, 6.8, and 7.3), and dust concentration (0, 10, 25, and 75 mg L^{-1}). Data are expressed as mean values ± SD ($n = 3$).

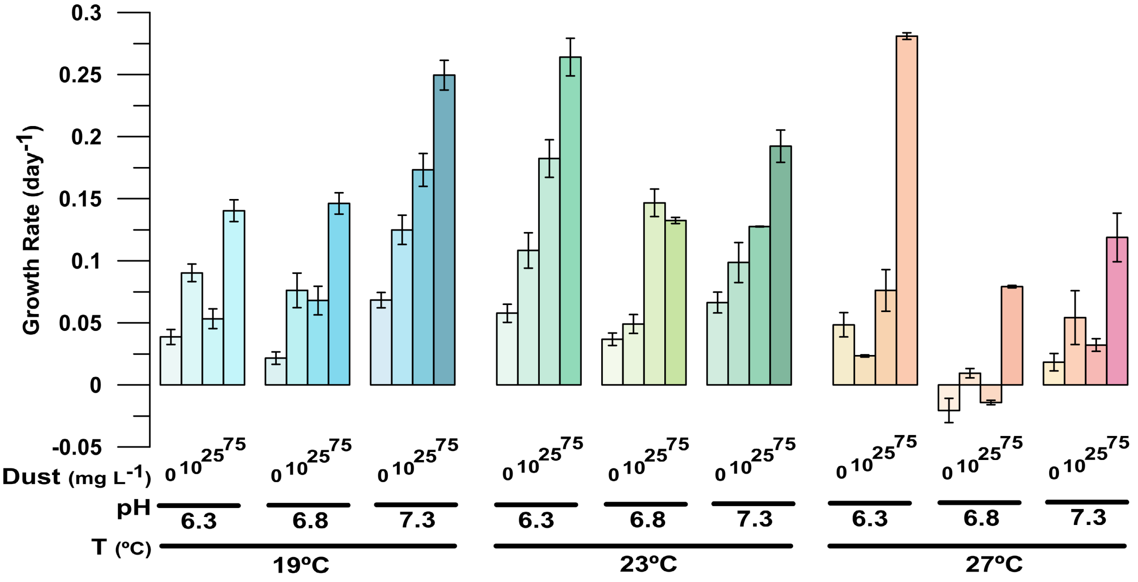

FIGURE 4 Maximum growth rate (day^{-1}) of *Scenedesmus obliquus* under different treatments of temperature (19, 23, and 27°C), pH (6.3, 6.8, and 7.3), and dust concentration (0, 10, 25, and 75 mg L^{-1}). Data are expressed as mean values ± SD ($n=3$).

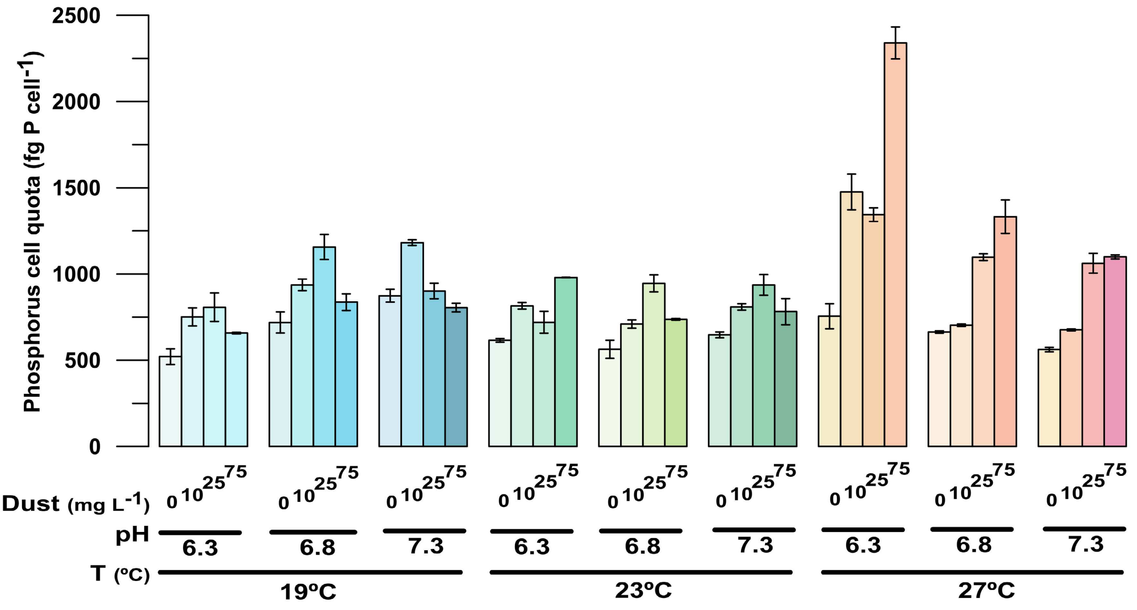

FIGURE 5 Phosphorous cell quota (fg P cell^{-1}) in *Scenedesmus obliquus* under different treatments of temperature (19, 23, 27°C), pH (6.3, 6.8, 7.3), and dust concentration (0, 10, 25, and 75 mg L^{-1}). Data are expressed as mean values ± SD ($n=3$).

be especially sensitive owing to low dust deposition rates. In contrast, some regions in northern Africa and the Arabian peninsula show a very low or zero impact of dust despite the high dust deposition due to the high pH of these soils (≥7.5).

4 | DISCUSSION

Our study investigates the role of dust-derived nutrients in stimulating phytoplankton growth and how dust affects their thermal and pH tolerance ranges. We develop a novel model for phytoplankton growth and test it using empirical data from a controlled experiment with *Scenedesmus obliquus*. The experiment included three temperature levels, three pH levels, and four dust concentrations. Our ecological model provides valuable insights into the future dynamics of phytoplankton populations and their responses to environmental conditions. We also forecast the potential impact of dust on freshwater ecosystems in continental areas, taking into account their sensitivity to acid deposition, soil pH, and the effects of global warming.

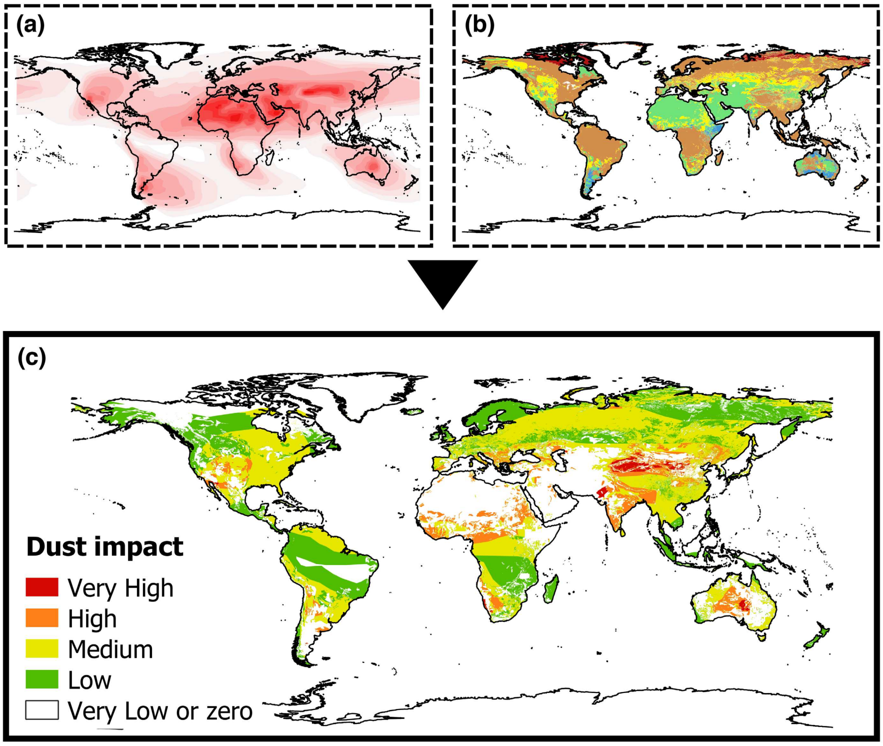

FIGURE 6 Composition of maps for world spatial analysis using mineral dust deposition ($\mathrm{g\,m^{-2}\,year^{-1}}$) obtained from Kok et al. (2021), where intensely red-colored regions indicate higher dust depositions (a); world regions potentially sensitive to dust inputs, where red-brown regions are more sensitive than yellow-green regions (b; see Figures S2–S5); and impact of dust in different regions (c) obtained from combination of map "a" and "b".

4.1 | Dust effect on growth

The positive effect of dust on *S. obliquus* growth rate and abundance observed in our study (P-limited environment; NP molar ratio = 75) is consistent with real world observational studies, and likely related to the alleviation of phosphorus (P) limitation (Camarero & Catalan, 2012), highlighting the potential of dust as a driver of primary production and phytoplankton growth (Ballantyne et al., 2011; Morales-Baquero et al., 2006), particularly in freshwater ecosystems of the western United States (Brahney, Ballantyne, et al., 2015), southern Europe (Cabrerizo et al., 2017; González-Olalla et al., 2018), as well as increasing phytoplankton biomass (Stockdale et al., 2016) and Chl *a* in marine areas of the Mediterranean sea (Gallisai et al., 2014; González-Olalla et al., 2017) South China Sea (Chu et al., 2018), or Tropical Atlantic Ocean and Southern Ocean (Barkley et al., 2019).

Our experiment revealed a complex relationship between temperature, pH, and dust concentration that aligns for the most part with the growth rate hypothesis, and highlights the importance of considering nutrient limitation and cellular processes in understanding the responses of microalgae to environmental changes. The growth rate hypothesis (Sterner & Elser, 2002) predicts that there is a positive relationship between maximum growth rate and P-rich RNA (expressed as $\mathrm{g^{-1}}$ dry weight). This positive relationship has been corroborated in successive studies with eukaryotic photosynthetic organisms, including freshwater microalgae ($R^2 = .66$; Rees & Raven, 2021). We found a similar pattern between the growth rate of *S. obliquus* and *P* cell quota, increasing from low to high pH at low temperature, and from high to low pH at the highest temperature. Remarkably, *S. obliquus* growing at 27°C, pH 6.3 and under dust addition of 75 mg dust $\mathrm{L^{-1}}$ showed the highest *P* cell quota in agreement with the highest growth rate. However, we found this relationship did not always hold true. Some treatments of 25 and 75 mg dust $\mathrm{L^{-1}}$ did not show a higher *P* cell quota according to a higher growth rate. We think that there are two possible explanations: that a high rate of cell division under these conditions can lead to high growth but also a lower amount of *P* per cell (Hoppe et al., 2018; Thompson et al., 1992; Wolf et al., 2018); or that the increased competitive ability of the bacteria present in the environment to acquire and store nutrients (Sterner et al., 2004) may have affected the availability of *P* for *Scenedesmus*. In nature, if the demand for *P* by the bacteria in the aquatic environment exceeds the *P* supplied by the dust, there could be a decrease in the magnitude of phytoplankton's response (Tanaka et al., 2006). However, in our experiment, the SRP values and *Scenedesmus* growth rate increased as the dust concentration in the medium increased, so we do not expect *Scenedesmus's* response to be conditioned by a high demand for *P* by the bacteria. In any case, we consider that changes in the magnitude of the phytoplankton response would not alter its direction or pattern of response.

On the other hand, it is important to note that composition of the dust sample used in our experiment and its effects on phytoplankton growth are representative of events in other parts of the planet. The phosphorus content in our sample (1113.86 mg P $\mathrm{kg^{-1}}$; 0.11% of *P* relative to the dust) falls within the intermediate range of Sahara Desert dust samples (0.022%–0.6%; see Gross et al., 2015, 2016, 2021; Guieu et al., 2002), similar to Colorado dust (0.055–0.091%; see Lawrence et al., 2010; Zhang et al., 2018), and very close to the mean concentration determined by Lawrence and Neff (2009) for 10 samples of dust deposited in different regions of the planet (1086.6 mg P $\mathrm{kg^{-1}}$), or even lower than Negev Desert dust (0.41–1.2%; see Gross et al., 2021; Uni & Katra, 2017), as well as dust enriched with ashes from wildfires (0.77–0.84%; see Tiwari et al., 2022), or dust collected near urban areas in Pakistan (1.6%; Shafqat et al., 2016). Furthermore, the fraction of bioavailable phosphorus over the total phosphorus, on average, was 30% in our dust, compared to 15% in North African aerosols (Dam et al., 2021) and 54% in European aerosols (Longo et al., 2014). Anderson et al. (2010) found that 15–30% of the phosphorus contained in dust from the Gulf of Aqaba was bioavailable. In the Negev Desert, this fraction only represented 8% of the total phosphorus (Gross et al., 2021), while in areas of Pakistan (Shafqat et al., 2016), the amount of bioavailable phosphorus exceeded that of our dust sample (895 $\mathrm{mg\,kg^{-1}}$ in Pakistan vs. 397 $\mathrm{mg\,kg^{-1}}$ in our dust; see Table S3). Therefore, considering the area covered by our collectors ($\approx 3\times10^6\,\mathrm{km^2}$), the duration of the dust collection period (6 months, Spring–Summer), the various sources of dust emissions that our collectors are capable of capturing (deserts, urban areas, wildfires), and the *P* richness of our dust sample, which is the primary limiting nutrient for phytoplankton growth in our experiment and most of freshwater ecosystems, we believe that the dust employed in our experiment provides a reasonably accurate approximation of its actual effects on freshwater phytoplankton.

In essence, we anticipate observing a similar response pattern, with variations in magnitude of effect (but not in direction), depending on the nutrient content of the dust. Despite that, we should note that in some cases dust could have a negative effect on phytoplankton growth if the presence of toxic metals outweighs the benefits of nutrient inputs (Paytan et al., 2009).

4.2 | Dust effect on thermal and pH tolerance range

One of our most compelling findings is that dust can play a critical role in broadening the environmental tolerances of phytoplanktonic organisms. Specifically, we found that dust is able to exert a positive effect on increasing the range of thermal and pH tolerance in a commonly found freshwater phytoplankton species, *S. obliquus*. In our experiments, *S. obliquus* showed the highest growth rate at 23°C, but its growth significantly declined at 27°C. Our growth model also shows that the optimum growth temperature ranged between 22 and 23°C under conditions of no dust addition. These results would agree with previous authors who have shown a greater growth of *Scenedesmus* around 25°C (see Yang et al., 2018). Remarkably, when we added increasing concentrations of dust the optimum temperature was increased and thermal tolerance widened for all the pH conditions (see Figure 2 and Table S4). Thus, optimum temperature (and upper thermal limit) in our Growth model varied from 22.94°C (27°C) under no dust addition to 24.66°C (30°C) after addition of 75 mg dust $\mathrm{L^{-1}}$ at pH 6.3. Similar changes but of lower magnitude were observed for pH 6.8 and 7.3. In our experiment, the addition of dust (75 $\mathrm{mg\,L^{-1}}$) counteracted the negative effect of high temperature and low pH and stimulated *S. obliquus* growth showing positive values at 27°C for all the pH conditions. Nutrient availability and temperature are key environmental factors that control phytoplankton growth and they can act synergistically stimulating the algal biomass (Fernández-González et al., 2022). Ectothermic organisms that exhibit increasing performance as temperature increases must also be able to supply nutrients and other resources to keep the high demand of biological rates (Kefford et al., 2022). If nutrient resources increase simultaneously to temperature increase, then optimum temperature for growth will increase and also the upper thermal limit will increase (Huey & Kingsolver, 2019). Therefore, nutrients contained in dust can supply the energy and nutritional building blocks so that phytoplankton is able to cope with temperature increase. In agreement with our results, Thomas et al. (2017) showed that higher concentration of nutrients leads to a broader thermal tolerance of the marine *Thalassiosira pseudonana*, and Bestion et al. (2018) reported that those findings can be generalized to six other freshwater phytoplankton species, including *S. obliquus*.

Our results also indicate that dust addition was able to increase the pH tolerance in *S. obliquus*. Under the no dust addition treatment, our results support the conclusion that a slightly alkaline environment is more favorable for the *Scenedesmus* growth (Al-Shatri Hussein et al., 2014; Gardner et al., 2011). Other studies have reported that a pH decrease exerts a negative effect on *S. obliquus* biomass in the range of 6–8 (Zhang et al., 2019). Therefore, in agreement with our growth model, we should expect a lower growth at pH 6.3 than at 7.3. In fact, *S. obliquus* growing at 19°C and no dust addition exhibited a significantly lower growth rate at pH 6.3 and 6.8 than at pH 7.3. However, when dust was introduced, our results show that the negative effect of low pH on phytoplankton growth becomes positive under high dust deposition (75 mg dust $\mathrm{L^{-1}}$) and high temperature, due to the positive effect of warming and nutrient availability on phytoplankton growth. Furthermore, the optimum temperature for growth and thermal tolerance exhibited a greater increase as the pH decreased from 7.3 to 6.3 and dust concentration increased from 0 to 75 $\mathrm{mg\,L^{-1}}$. Our results for *Scenedesmus* confirmed that at 27°C and a pH of 6.8 or 6.3, the highest addition of dust exerted a positive effect on growth rate, counteracting the negative effect of pH 6.8 on phytoplankton under no dust addition and showed the highest growth rate at pH 6.3 for all the treatments.

It is possible that the greater availability of *P* at low pH could explain a synergistic interaction between temperature and nutrients. In fact, our nutrient model, supported by the dust *P* release results obtained in our experiment, shows that a decrease in pH led to higher available *P* concentrations for each dust and temperature treatment (Figure 3). Previous research has indicated that acidic conditions during the transport of dust in the atmosphere can increase the bioavailability of P, thereby increasing the potential for dust to exert a strong effect in oligotrophic ecosystems (Baker & Croot, 2010; Stockdale et al., 2016). Additionally, when a scarcity of inorganic phosphorus coincides with a mildly acidic pH, it can promote the stimulation of acid phosphatase activity (optimal pH 4–6), further increasing the bioavailability of *P* (Hoppe, 2003). While the pH reduction applied in our experiment does not reach the acidity levels associated with extreme levels of sulfuric and nitric acid in the atmosphere, our findings demonstrate that a pH decrease of 0.5–1 units in aquatic ecosystems was able to increase the *P* released from dust. In contrast, Dinasquet et al. (2022) reported that a pH decrease of 0.3 units under warming conditions did not affect the amount of nutrient released from dust. However, their experiment was carried out with a marine community, so it is possible that a high initial pH of the seawater (ca. 8.2) combined with a limited decrease of pH compared to our experiment affected the nutrient release. That means that because freshwater ecosystems have in general lower pH and buffering capacity, particularly when they are significantly affected by acid deposition, they can experience greater impacts from dust inputs. Despite the main goal of this study being to assess how initial pH conditions can affect nutrient release from dust and its subsequent impact on algal growth, we should also mention that dust, often rich in alkaline constituents, can alter pH levels in aquatic ecosystems (Brahney et al., 2014, 2021; Rogora et al., 2004), leading to changes in the carbonate system and nutrient availability that could influence phytoplankton growth (Galotti et al., 2018). However, this falls outside the scope of our study and undoubtedly warrants further consideration in future models and experiments.

Our innovative study examines the interactions between dust, pH, and warming. We demonstrate that in aquatic systems experiencing high dust inputs and warming conditions, a decrease in pH of up to 1 unit can exert a positive effect on phytoplankton attributed to an extra release of nutrients available for growth. In contrast, a previous study by Murphy et al. (2020) showed a negative effect on phytoplankton from rock pools when subjected to warming (+8°C) and acidification of 0.8 units. In our research, we not only corroborate the role of dust increasing the thermal range and temperature optimum in phytoplankton, but we also demonstrate that a negative effect of lower pH under low nutrient concentrations can be transformed to a positive effect due to a higher release of nutrients from dust under more acidic conditions. This interaction becomes particularly significant when combined with higher temperatures, broadening the pH range suitable for growth and influencing the competitive ability of different phytoplankton species (Hansen, 2002). It is important to note that this positive effect of the pH has a species-specific limit that corresponds to their pH tolerance range (Hinga, 2002). A more substantial decrease in pH could have detrimental consequences on cellular functioning that would not be compensated for an excess of nutrients. In essence, while the theoretical growth curves of phytoplankton in response to these factors are common across species, and thus show a realistic approximation of our study, the different optimal ranges for temperature, pH, and nutrients are species specific and reinforce the need for further research involving a larger number of key phytoplankton species.

4.3 | Dust effect on a global scale

Geospatial modeling indicates that areas of the planet most vulnerable to atmospheric dust deposition are generally situated near arid and semi-arid areas, especially if the land is degraded or under unsustainable use (Ginoux et al., 2012). Therefore, regions such as the western United States, areas near the Atacama Desert in South America, central and southern Africa and Asia, central Australia as well as the Mediterranean region will be highly or very highly impacted by dust deposition.

Our experimental results suggest that the impact of dust on continental aquatic ecosystems, and more specifically on phytoplankton, will be determined by the amount and composition of dust, the degree of oligotrophy of the water (Marañón et al., 2010; Marín-Beltrán et al., 2019), the initial composition and metabolic state of the investigated community (Gazeau et al., 2021), as well as by the characteristics of the underlying ecosystems (e.g., soil properties including pH, cation exchange capacity, or bedrock; Likens et al., 1996; Nadelhoffer et al., 1999). Therefore, the spatial variability of freshwater conditions will determine the magnitude of dust impact to lake ecosystems. Although our geospatial analysis could not directly determine the metabolic state of each lake, we used the geologic properties of the basins to estimate the natural condition and thus the future impact of increasing temperature and dust additions. Because physicochemical factors of aquatic ecosystems, such as pH, strongly affect *P* behavior after dust deposition, we found that areas with calcareous bedrock, and hence higher pH (Lazzaro et al., 2009; Mosher & Findlay, 2011), required more dust addition to alter the aquatic community than sites in more siliceous bedrock (Figure 6). While most of the *P* contained in Saharan dust is released in the Amazon basin due to its highly acidic soils (pH 4.17–4.94) (De Negreiros & Nepstad, 1994), only 15–30% of *P* reaching the Gulf of Aqaba (Anderson et al., 2010) is released from dust because of the alkaline seawater (pH ≈ 8.2). Accordingly, basins with low pH or low CEC, and where a strong increase in temperature is expected were potentially very sensitive to dust impacts.

Climate projections suggest that current dusty regions are likely to experience a decrease in precipitation, including the southwest of United States, southern Australia, Mediterranean area, northern Sahara, and central Asia (Christensen et al., 2007). Furthermore, drought conditions and landscape disturbance will increase dust emissions to the atmosphere as well, due to its effect on soil moisture and vegetation coverage (Munson et al., 2011; Prospero & Lamb, 2003). Therefore, our analysis allows us to point out the areas of the planet that may be exposed to a greater impact of dust, altering the functioning of the dynamics of populations and ecosystems in those regions.

5 | CONCLUSIONS

Our work attempts, for the first time, to analyze and describe the complex interaction of how the foreseeable increase in dust storms and the input of nutrients to aquatic ecosystems can interact together with temperature and pH leading to a regulation of the phytoplankton growth rate growing in freshwater aquatic communities. Our empirical results and our mechanistic model show that dust storms are capable of stimulating phytoplankton growth and that high intensity storms can broaden the range of thermal and pH tolerance in the phytoplankton. Thus, phytoplanktonic organisms located in ecosystems where dust deposition can supply limiting nutrients (e.g., phosphorus) may show a greater capacity for acclimation under future conditions of higher temperatures and low pH. This response is possible because phytoplankton can utilize the additional nutrient supply resulting from a slight drop in pH, combined with high temperatures, to promote their growth. Our findings emphasize the importance of comprehending the factors that regulate phytoplankton population dynamics and employing mechanistic models to explain and interpret these responses. Furthermore, our research illustrates how dust can impact the organisms at the foundation of aquatic food webs, influencing the role of aquatic ecosystems in biogeochemical cycles (e.g., carbon sink) and the management of biological resources in highly dust-sensitive aquatic ecosystems.

AUTHOR CONTRIBUTIONS

Juan Manuel González-Olalla: Conceptualization; data curation; formal analysis; investigation; validation; visualization; writing – original draft; writing – review and editing. **James Powell:** Conceptualization; formal analysis; supervision; visualization; writing – review and editing. **Janice Brahney:** Conceptualization; funding acquisition; supervision; writing – review and editing.

ACKNOWLEDGMENTS

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. The authors are grateful to Audree Provard for her help in the analysis of soluble reactive phosphorus and Karin Kettenring for letting us use the environmental chambers for the experiment.

CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The data and model code that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.10116443, *reference number 10116443*.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: González-Olalla, J. M., Powell, J. A., & Brahney, J. (2023). Dust storms increase the tolerance of phytoplankton to thermal and pH changes. *Global Change Biology*, *30*, e17055. https://doi.org/10.1111/gcb.17055