JGR Biogeosciences

RESEARCH ARTICLE
10.1029/2023JG007954

Key Points:

- Dust collected by *Trichodesmium* colonies from seawater as a nutrient source may result in metal toxification and buoyancy loss
- At moderate dust loads, colonies kept their buoyancy, but above 400 ng, sinking velocities increased linearly with dust loads
- Desert dust induced *Trichodesmium* mortality through toxic metal release, yet the lethal dose far exceeded oceanic dust concentrations

Supporting Information:

Supporting Information may be found in the online version of this article.

Correspondence to:

S. Wang and Y. Shaked,
siyuan.wang@mail.huji.ac.il; yeala.shaked@mail.huji.ac.il

Citation:

Wang, S., Zhang, F., Koedooder, C., Qafoku, O., Basu, S., Krisch, S., et al. (2024). Costs of dust collection by *Trichodesmium*: Effect on buoyancy and toxic metal release. *Journal of Geophysical Research: Biogeosciences*, *129*, e2023JG007954. https://doi.org/10.1029/2023JG007954

Received 7 DEC 2023
Accepted 1 APR 2024

Author Contributions:

Conceptualization: Siyuan Wang, Yeala Shaked
Data curation: Siyuan Wang
Formal analysis: Siyuan Wang, Futing Zhang, Coco Koedooder, Odeta Qafoku, Subhajit Basu, Stephan Krisch, Anna-Neva Visser, Meri Eichner, Nivi Kessler
Funding acquisition: Rene M. Boiteau, Martha Gledhill, Yeala Shaked
Methodology: Siyuan Wang, Futing Zhang, Odeta Qafoku, Subhajit Basu, Stephan Krisch, Anna-Neva Visser
Supervision: Yeala Shaked

Costs of Dust Collection by *Trichodesmium*: Effect on Buoyancy and Toxic Metal Release

Siyuan Wang[1,2], Futing Zhang[1,2], Coco Koedooder[1,2,3], Odeta Qafoku[4], Subhajit Basu[1,2,5], Stephan Krisch[6], Anna-Neva Visser[1,2], Meri Eichner[7], Nivi Kessler[1,2,8], Rene M. Boiteau[9], Martha Gledhill[6], and Yeala Shaked[1,2]

[1]The Freddy and Nadine Herrmann Institute of Earth Sciences, Edmond J. Safra Campus, Givat Ram, Hebrew University of Jerusalem, Jerusalem, Israel, [2]The Interuniversity Institute for Marine Sciences in Eilat, Eilat, Israel, [3]Israel Limnology and Oceanography Research, Haifa, Israel, [4]Environmental Molecular Sciences Laboratory (EMSL), Pacific Northwest National Laboratory (PNNL), Richland, WA, USA, [5]University of Petroleum and Energy Studies (UPES-SoHST), Energy Acres, Dehradun, India, [6]GEOMAR, Helmholtz Center for Ocean Research, Kiel, Germany, [7]Center Algatech, Institute of Microbiology of the Czech Academy of Sciences, Třeboň, Czech Republic, [8]Now at the Water Authority, Jerusalem, Israel, [9]Department of Chemistry, University of Minnesota, Minneapolis, MN, USA

Abstract The marine cyanobacterium *Trichodesmium* has the remarkable ability to interact with and utilize air-borne dust as a nutrient source. However, dust may adversely affect *Trichodesmium* through buoyancy loss and exposure to toxic metals. Our study explored the effect of desert dust on buoyancy and mortality of natural Red Sea puff-shaped *Trichodesmium thiebautii*. Sinking velocities and ability of individual colonies to stay afloat with increasing dust loads were studied in sedimentation chambers. Low dust loads of up to ~400 ng per colony did not impact initial sinking velocity and colonies remained afloat in the chamber. Above this threshold, sinking velocity increased linearly with the colony dust load at a slope matching prediction based on Stoke's law. The potential toxicity of dust was assessed with regards to metal dissolution kinetics, differentiating between rapidly released metals, which may impact surface blooms, and gradually released metals that may impact dust-centering colonies. Incubations with increasing dust concentrations revealed colony death, but the observed lethal dose far exceeded dust concentrations measured in coastal and open ocean systems. Removal of toxic particles as a mechanism to reduce toxicity was explored using SEM-EDX imaging of colonies incubated with Cu-minerals, yet observations did not support this pathway. Combining our current and former experiments, we suggest that in natural settings the nutritional benefits gained by *Trichodesmium* via dust collection outweigh the risks of buoyancy loss and toxicity. Our data and concepts feed into the growing recognition of the significance of dust for *Trichodesmium*'s ecology and subsequently to ocean productivity.

Plain Language Summary *Trichodesmium* spp. are abundant cyanobacteria, forming extensive blooms in low latitude warm oceans, and contribute significantly to carbon (C) and nitrogen (N) fixation, recycling and export. Desert dust deposited on the ocean surface was shown to supply *Trichodesmium* with the scarce micronutrient iron. Spherical, millimeter-sized colonies of *Trichodesmium* from different ocean basins were reported to actively accumulate dust in their cores. While dust accumulation likely helps *Trichodesmium* obtain nutrients, it may come at a cost. Metals released from dust may induce toxicity and the dust weight could send *Trichodesmium* to the ocean depth. Our experimental study with natural Red Sea colonies examined some trade-offs of dust accumulation. Links between dust load and colony buoyancy were examined in sedimentation experiments. Toxicity thresholds for surface blooms and dust-accumulating colonies were determined from mortality assays and dust dissolution measurements. We found that metal-induced toxicity to *Trichodesmium* is unlikely at typical oceanic dust fluxes, and that dust-containing colonies can remain buoyant. At high loads, dust weight determined the colony's sinking velocity. Our findings and concepts can be extended to additional aerosols and *Trichodesmium*-rich habitats, and may assist in assessing *Trichodesmium*'s distribution, ecophysiology, and contribution to C or N transport to the deep ocean.

1. Introduction

Trichodesmium spp. is a filamentous, N_2-fixing, bloom-forming cyanobacterium, inhabiting subtropical and tropical oligotrophic ocean regions, contributing ~40% of the annual global marine nitrogen fixation (Capone et al., 1997; Tang et al., 2020; Zehr & Capone, 2020). *Trichodesmium* spp. appear as both, individual filaments (trichomes) and colonies, containing hundreds to thousands of trichomes organized in millimeter-sized tuft- or

Writing – original draft: Siyuan Wang, Yeala Shaked
Writing – review & editing: Futing Zhang, Coco Koedooder, Odeta Qafoku, Subhajit Basu, Stephan Krisch, Anna-Neva Visser, Meri Eichner, Nivi Kessler, Rene M. Boiteau, Martha Gledhill

puff-shaped aggregates (Eichner et al., 2023). In the Red Sea, puff-shaped colonies are primarily composed of *Trichodesmium thiebautii*, while tuft-shaped colonies are typically comprised of *Trichodesmium erythraeum* (Koedooder et al., 2022). The different colony morphologies also serve as micro-habitats for diverse microbes including bacteria, phytoplankton and even zooplankton, all exchanging nutrients and carbon throughout the colony life cycle from growth to demise (Anderson, 1977; Frischkorn et al., 2018; Lee et al., 2017; Rouco et al., 2016).

Natural *Trichodesmium* is often limited, or co-limited, by iron (Fe) and phosphorus (P) (Cerdan-Garcia et al., 2022; Held et al., 2020). Aerosol dust deposited on the ocean surface is considered an important nutrient source, but the low solubility of Fe and P minerals restrict their bioavailability for phytoplankton (Mills et al., 2004; Shaked et al., 2023; Shaked & Lis, 2012; Stockdale et al., 2016). Incubation studies revealed that *Trichodesmium* successfully grow on aerosol or dust (Chen et al., 2011; Polyviou et al., 2018), and even increase the bioavailability of dust-borne Fe and P (Basu et al., 2019; Basu & Shaked, 2018; Shaked et al., 2023). An intriguing finding, which was reaffirmed in several studies, is the ability of *Trichodesmium* colonies to actively collect and transport dust particles into the colony core (Kessler, Armoza-Zvuloni, et al., 2020; Rubin et al., 2011; Wang et al., 2022). Particle centering may not only enhance dust dissolution, but could also minimize nutrient loss by diffusion, and thus optimize uptake (Eichner et al., 2023; Shaked et al., 2023). While these nutritional benefits are well established, studies exploring negative sides of particle collection to *Trichodesmium,* remain scarce. Collection of heavy dust minerals may result in buoyancy loss and accelerate sinking to the deep ocean (Held et al., 2022; Pabortsava et al., 2017). Dust also contains an array of toxic elements (Bozlaker et al., 2013; Mackey et al., 2015), which, upon gradual release within the colony core, may induce toxicity and cause mortality. Our study focuses on this “dark side” of particle collection by, firstly, investigating the effect of dust on buoyancy and trace metal exposure of *Trichodesmium* spp. and, secondly, examining active particle removal.

Depending on composition, dust particle density was reported to range from 2.1 to 2.6 $g \cdot cm^{-3}$ (McConnell et al., 2008; Schladitz et al., 2009), much denser than *Trichodesmium* with density of ~1 $g \cdot cm^{-3}$ (Kromkamp et al., 1992; White et al., 2006). Consequently, collection of dust particles by *Trichodesmium* spp. colonies increases their density and may affect *Trichodesmium*'s buoyancy. *Trichodesmium* spp. regulates its buoyancy through gas vesicles which can withstand high pressures (up to 12–37 bars, Walsby, 1992). This allows *Trichodesmium* to float on the water surface while also being able to resist hydraulic forces (Walsby, 1992). While in the Gulf of Aqaba *Trichodesmium* typically appears as colonies (Post et al., 2002; Wang et al., 2022), in other oceanic regions it may occur predominantly as positively buoyant free trichomes, or as a mix of colonies and free trichomes (e.g., Eichner et al., 2023; Pierella Karlusich et al., 2021). In addition, Villareal and Carpenter (2003) found that ~90% of the colonies they measured were positively buoyant. Thus, healthy natural *Trichodesmium* populations in the surface ocean are considered to be neutrally or positively buoyant (Villareal & Carpenter, 1990; Walsby, 1992). Most observations of *Trichodesmium* were made within mixing layer depth (MLD) and euphotic zone (Rouco et al., 2014; Tyrrell et al., 2003). *Trichodesmium* has also been observed in the mesopelagic zone, while maintaining its capability to fix N_2 (down to ~1,000 m, Benavides et al., 2022), or as intact colonies in deep sediment traps (3,000 m, Pabortsava et al., 2017). Intriguingly, these deep colonies were observed to contain dust particles (Pabortsava et al., 2017). As suggested by model-based studies (Kromkamp et al., 1992; White et al., 2006), *Trichodesmium* has the ability to conduct vertical migration to several hundred meters. While a recent study modeled the effect of dust on sinking velocities of *Trichodesmium* (Held et al., 2022), experimental evidence linking dust loads and sinking velocities are missing. Besides dust, other factors, such as light availability and colony morphology, strongly influence the buoyancy regulation of *Trichodesmium* (Held et al., 2022; Villareal & Carpenter, 2003; Walsby, 1992). For example, the general population of *T. thiebautii* becomes more negatively buoyant during the day and more positively buoyant at night in diel cycles, due to changes in the carbohydrate to protein content within cells (Held et al., 2022; Villareal & Carpenter, 2003). Colony morphology also affects buoyancy, with different strengths and arrangements of gas vesicles varying among *Trichodesmium* species (e.g., turgor pressure for collapsing gas vesicles is 12 bar for *T. erythraeum* compared to 37 bar for *T. thiebautii*, Janson et al., 1995; Lundgren et al., 2005). These factors contribute to complex parameterizations for colony sinking models and further investigations are required to constrain those effects on the colony buoyancy.

Dust and other aerosols contain an array of elements, some of which are required as nutrients, while others such as cadmium (Cd), copper (Cu), lead (Pb) and arsenic (As) can be toxic (Guo et al., 2022; Mackey et al., 2012; Paytan et al., 2009; Yang et al., 2019). The potential toxicity of dust (or other aerosols) to *Trichodesmium* spp. depends on the kinetics of toxic metal release to seawater, which in turn vary with aerosol types and sources, reactions occurring during atmospheric transport and particle to solvent ratios (Mackey et al., 2015; Mahowald et al., 2018; Stockdale et al., 2016). Natural populations of *Trichodesmium* colonies are reported to be very sensitive to toxic metals such as Cu and As (Hewson et al., 2009; Rueter et al., 1979). In addition to metals released from dust to the seawater surrounding natural *Trichodesmium*, the collection of dust within colonies further exposes them to toxic metals which gradually dissolve from the particles. However, dust toxicity to *Trichodesmium*, especially at the level of individual colonies, is poorly understood.

Our study ventures to the "dark side" of particle collection by investigating the effect of dust on buoyancy and trace metal exposure of *Trichodesmium*. Hypothesizing that overload of dust particles collected by *Trichodesmium* colonies may lead to buoyancy loss and metal toxification, two sets of experiments with natural *Trichodesmium* colonies were conducted: (a) sedimentation experiments with single colonies artificially loaded with dust, and (b) incubations with increasing dust concentrations probing mortality and metal release rates. The ability of *Trichodesmium* to mitigate these effects through particle removal was also examined. This research highlights potential trade-offs associated with particle collection and may contribute to predicting *Trichodesmium's* vertical distribution and role in C and N export to the deep ocean.

2. Material and Methods

2.1. Colony and Dust Collection

Trichodesmium spp. colonies were collected from the Gulf of Aqaba (29.56°N, 34.95°E) at the Northern Red Sea during 2018–2022 via morning net tows (09:00–12:00). Each tow was conducted for ~7 min at the boat's minimal speed (1–2 knots) by deploying a 100 μm phytoplankton net equipped with a 100 μm cod end (Aquatic Research Instrument, USA) to 10–20 m depth. The net concentrate was diluted into ~5 L seawater to minimize stress and well-shaped puff colonies were quickly hand-picked by droppers, placed in clean Petri dishes and washed three times with 0.22 μm filtered seawater (FSW). Hydrographic data at the time of sampling were obtained by the Israel National Monitoring Program at the Gulf of Eilat (National monitoring program [Data set], 2024). Water temperature at the collection depth (10–20 m) ranged from 22.5 to 26.5°C, and the euphotic zone extended to a depth of 70–90 m. In springs the water column was stratified, while in autumns the mixed layer depth (MLD) reached 80–160 m. Phosphate (PO_4^{3-}), ammonium (NH_4^+), nitrite (NO_2^-) and nitrate (NO_3^-) concentrations at the time of sampling were low, ranging 20–80, 15–30, 3–20 and 20–60 nM, respectively. Dissolved iron (dFe) concentration was estimated at 1–2 nM (Shaked, 2008). Dust samples were collected from the Gulf of Aqaba shores at the Interuniversity Institute for Marine Sciences in Eilat (IUI). Samples of settled dust were collected from plastic surfaces located ~2 m from the sea, sieved through a 63 μm mesh, air-dried and stored in a desiccator.

2.2. Effect of Dust Load on Colony Buoyancy

2.2.1. Sedimentation Experiments

During autumn 2020, sedimentation experiments were conducted on five consecutive days in the afternoon, on each testing five different colonies. Puff-shaped *T. thiebautii* colonies were selected for sedimentation experiments due to the ease of manipulating dust loads on the colony and the reduced loss of dust during transfer, as compared to tuft-shaped colonies. Since colonies were exposed to low light (~40 μmol m^{-2} s^{-1}) for 3–6 hr prior to the experiments, they may have accumulated carbon ballast that resulted in a negative buoyancy (Villareal & Carpenter, 2003). Sinking velocities were measured in 18 cm tall sedimentation chambers (100 mL glass cylinders with 2.5 cm diameter) at 25°C and in the light at the intensity of ~40 μmol m^{-2} s^{-1}. Colonies were gently introduced to chambers filled with fresh seawater and their vertical positions were recorded over time (see a schematic diagram and further details in Supporting Information S1: Figure S1). Two types of data were collected: Initial colony sinking velocity in the chamber, as well as colony position in the chamber after 15 min. Each colony was tested three times: as is, following interactions with medium and then high dust concentrations. All colonies sank initially, hence sinking velocities were always positive. However, after 15 min colonies appeared to adjust their buoyancy and resumed different positions in the chamber. The ones at the bottom of the sedimentation chamber were defined as "sinkers" and the ones further up in the water as "floaters". Sinkers were not able to regain buoyancy, whereas floaters either achieved neutral buoyancy and maintained specific positions or were moving up and down in the chamber. In an additional experiment conducted on autumn 2020, the frequency of "sinkers" and "floaters" in freshly collected colonies ($n = 487$) was determined using the same method.

The result showed that 10% of the total colonies were "sinkers", while 90% of the colonies were positively buoyant at 15 min. Colony-dust interactions were induced by gently and repetitively mixing colonies within an eppendorf vial which contained seawater with the respective amount of dust. The dust load (weight) on each colony was calculated from stereoscopic images taken prior to introducing the colonies to the sedimentation chamber. Since many colonies lost dust particles during the experiments, another image was taken at the end of each experiment and dust weight was re-calculated.

2.2.2. Estimation of Colony Dust Loads

Dust load (weight) was estimated from colony images taken with a stereoscope (Nikon, SMZ745). Using DinoCapture 2.0 and ImageJ software, the area of dust centered by the colony (μm^2) was estimated. This area was converted to volume (μm^3) assuming a constant thickness of 10 μm for the dust layer and then to mass using an average density of 2.5 $g{\cdot}cm^{-3}$ (see Supporting Information S1 for details: Figure S2; Kessler, Kraemer, et al., 2020). Similar analysis was done on published images of dust-containing colonies (Held et al., 2021).

2.2.3. Calculating the Effect of Dust on Colony Sinking Velocities

Stoke's law, and its modified equations, have been widely applied in calculating and modeling sinking velocities of marine aggregates including natural *Trichodesmium* colonies (Kromkamp & Walsby, 1990; Laurenceau-Cornec et al., 2020; White et al., 2006). Recently, several attempts were made to assess the density change induced by internal ballasts (Benavides et al., 2022; Held et al., 2022). When colonies collect dust, not only their mass needs to be considered but also their volume. To account for both, dust mass and volume, the Stoke's law-based equation, adapted for *Trichodesmium* by White et al. (2006), was modified (see Supporting Information S1: Text S1). Based on this modified equation, the colony sinking velocity is predicted to increase linearly with dust load:

$$\begin{aligned}\text{Sinking velocity}_{(\text{dust-loaded colony})}\ \left(\text{m}\cdot\text{d}^{-1}\right) &= \text{Sinking velocity}_{(\text{dust-free colony})}\ \left(\text{m}\cdot\text{d}^{-1}\right) + \text{K}\left(\text{m}\cdot\text{d}^{-1}\cdot\text{ng}^{-1}\right)\\ &\quad\times \text{dust weight (ng)}\end{aligned} \tag{1}$$

The dust factor (K) is the velocity increase per dust mass with a unit of $m{\cdot}d^{-1}\ ng^{-1}$. Applying the measured colony size and the density of dust, Red Sea seawater and *Trichodesmium* cells (Basu & Shaked, 2018; Benaltabet et al., 2022; McConnell et al., 2008; Schladitz et al., 2009; White et al., 2006), we calculated that $K = 0.02$–0.06 ($m{\cdot}d^{-1}\ ng^{-1}$) (see Supporting Information S1: Text S2).

2.3. Metals in Dust and Toxicity to *Trichodesmium*

2.3.1. Dust Dissolution Experiments

Dust dissolution experiments were conducted in four separate experiments during 2015, using trace metal clean procedures, as described in Basu et al. (2019) and Gledhill et al. (2019). Local Red Sea dust was added to acid-cleaned Nalgene bottles containing gravimetrically quantified filtered seawater at final concentrations of 2 and 10 $mg{\cdot}L^{-1}$ and incubated at 25°C for 62 hr. 60 mL sub-samples were filtered through 0.22 μm syringe-filters (PVDF, Millex) using a Dynamax (Rainin) 8-head peristaltic pump under a clean bench. Sub-samples were stored for 6 months in trace metal cleaned high density polyethylene (HDPE) bottles and acidified to pH ~1.7 with ultra-clean HNO_3 prior to analysis of metals. Metals were analyzed by inductively coupled plasma mass spectrometry after preconcentration (SeaFAST pico) following the method of Rapp et al. (2017), and were quantified by standard addition (Krisch et al., 2022) at GEOMAR, Helmholtz Center for Ocean Research, Kiel, Germany. Extending our experiments we also included dissolution measurements of local Red Sea dust samples from Mackey et al. (2015). We then split the dissolution data to two groups: (a) rapid dissolution (10 min and 6 hr), and (b) gradual dissolution (1, 3 and 7 days).

2.3.2. Toxicity Assays

Dust toxicity was investigated by incubating ~180 individual natural *Trichodesmium* colonies for 24 hr in 48 well-plates with either dust suspension or dust leachate. Primary dust suspension was prepared daily in FSW and diluted to final concentrations of 2, 10, 100, 500, and 1,000 $mg{\cdot}L^{-1}$. Dust leachates were obtained after 10 min by filtering the dust suspensions through 0.22 μm syringe-filters (PC membrane). Colonies were incubated in wells of a 48-well plate containing 0.5 mL dust suspension or leachate, and were kept in a culture room (25°C, ∼80 μmol m^{-2} s^{-1}, 10:14 hr light-dark cycle). Visual changes of the colony and filament shape, structure, and color were monitored under a stereoscope at 2, 5, and 24 hr (see Supporting Information S1: Text S4). Incubation experiments were restricted to 24 hr due to significant mortality observed across all treatments beyond this timeframe. The 24 hr duration proved sufficient for assessing the impact of dust on colony mortality, as suggested by preliminary experiments spanning 0–72 hr (see Supporting Information S1: Figure S6). Incubations were repeated twice during spring 2022 and included controls without dust additions. Probing specifically for Cu toxicity, colonies were also incubated with dissolved Cu (5–3,000 nM $CuSO_4$, see Supporting Information S1: Text S4).

2.4. Removal of Cu-Containing Minerals

Hypothesizing that colonies may remove toxic minerals as a detoxification mechanism, 16 Red Sea colonies were incubated with the Cu mineral malachite ($Cu_2CO_3(OH)_2$). To ensure optimal colony-mineral interactions, malachite was mixed with hematite (α-Fe_2O_3), which is typically preferred by *Trichodesmium* (Kessler, Armoza-Zvuloni, et al., 2020). Individual colonies were sampled at different time points, placed on filters and probed for the presence of malachite via light microscopy and scanning electron microscopy with energy dispersive X-Ray analysis (SEM-EDX). Experiments were repeated for three days in autumn 2021. Malachite was obtained from Timna National Park (Eilat, Israel), crushed and sieved (<38 μm), while hematite (<38 μm) was obtained from the Mineral Collection at the National Natural History Collections at the Hebrew University of Jerusalem, Israel. Colonies were incubated in Eppendorf vials under the IUI pier up to 24 hr. At three time points, randomly selected colonies were imaged and placed on a PES membrane filter (Supor®), air-dried and frozen prior to SEM-EDX analysis (see Supporting Information S1: Text S5 for full details).

2.4.1. Microscopic SEM-EDX Imaging

Colonies were placed on Supor® filters and coated with a ∼10 nm carbon layer by thermal evaporation using a 108C Auto Carbon Coater (Ted Pella, Inc.) to avoid charging during the analysis. SEM images were collected with a FEI Helios NanoLab 600i field emission electron microscope. Specimen morphology was examined using a secondary electron Everhart-Thornley detector (ETD) in a field free mode at an acceleration voltage of 3 kV and a probe of 86–170 pA at 4 mm working distance. EDX analysis was performed at 10–20 kV and 1–2 nA with an X-Max 80 mm^2 Silicon Drift Detector (SDD) from Oxford Instruments. Oxford AZtec software was used to collect compositional maps and point spectrum analyses.

3. Results and Discussion

3.1. Dust Loads and Buoyancy Control

Collection and centering of dust particles by *Trichodesmium* colonies may result in buoyancy loss and enhance their sinking velocities to the ocean depth. In the following section we present experimental results of natural colonies that were interacted with dust and tested in sedimentation chambers. The impact of dust on the colony buoyancy was examined by two different measures: (a) initial, short-term (∼5 min) sinking velocity, and (b) colony position in the chamber after a 15 min acclimation period. All colonies had positive initial sinking velocities, but within 15 min some colonies left the chamber bottom and were re-suspended in the water. Colonies that remained on the bottom were considered as non-buoyant ("sinkers"), while those in the water were considered as buoyant ("floaters").

3.1.1. How Much Dust Can a Colony Bear to Stay Afloat?

At low dust loads (<100 ng) half of the colonies were classified as "floaters" (Figure 1, orange symbols). At intermediate dust loads of 100–1,000 ng, the fraction of "floaters" dropped but still accounted for ∼30% of the colonies (Figure 1, orange symbols). These findings demonstrate a remarkable ability of *Trichodesmium* to adjust their buoyancy to accommodate a significant dust load, assisted by their gas vesicles (Walsby, 1992). At increasing dust loads, and especially above 1 μg dust per colony, most colonies were defined as "sinkers" (Figure 1, blue symbols), indicating a limit to *Trichodesmium*'s capacity to adapt its buoyancy.

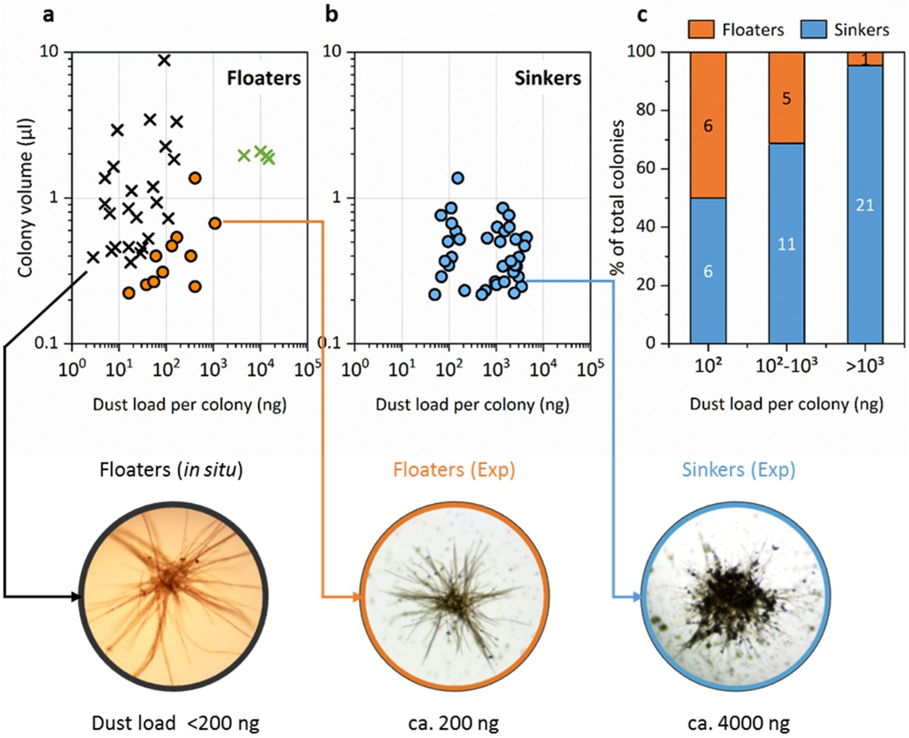


Figure 1. Effect of dust load on the buoyancy of natural *Trichodesmium* colonies. Data compilation from natural colonies either containing particles when collected (crosses) or interacted with dust and tested in sedimentation experiments (circles). Colonies were categorized as "floaters" or "sinkers" according to their position in sedimentation chambers after 15 min. In situ colonies were defined as "floaters" since they were collected from the upper water column for 10–20 m depth. (a) Range of dust loads associated with "floater" colonies tested in sedimentation experiments ($n = 12$, orange circles) and freshly collected from the Red Sea ($n = 24$, black crosses) and the Atlantic Ocean ($n = 4$, green crosses, images from Held et al., 2021). (b) Range of dust loads associated with "sinker" colonies tested in sedimentation experiments ($n = 38$, blue circles). (c) Fraction of experimentally determined "floaters" and "sinkers" as a function of dust load per colony. Pictures show typical dust loads as quantified through image analysis.

Expanding the experimental data to natural conditions, dust loads associated with Red Sea *Trichodesmium* colonies collected from the upper 10–20 m during 2018/19 were analyzed. These colonies were considered buoyant since they populated the upper water column and were plotted together with the experimentally determined "floaters" (Figure 1a). Each colony typically contained 1–7 particles in sizes ranging between 10 and 70 µm in diameter (see Supporting Information S1: Table S1). The calculated weight of these particles amounted to 3–170 ng per colony and did not correlate with the colony volume (Figure 1a, black crosses). These estimated dust-loads of floating, naturally occurring colonies, matched our experimental findings (Figure 1a, orange circles). Similar weights of 200–300 ng dust per colony were also reported by Kessler, Kraemer, et al. (2020), who analyzed SEM images of colonies collected from the upper 20 m of the Gulf of Aqaba (Kessler, Kraemer, et al., 2020). Interestingly, the Red Sea colonies fall short compared to Atlantic colonies collected from 20 m depth, which are known to remain afloat although carrying much higher particle loads (Bif & Yunes, 2017; Held et al., 2021). Analyzing single colony images from the study of Held et al. (2021), we calculated dust loads of up to 10 µg per colony (Figure 1a, green crosses). The ability to keep afloat with a higher dust load may stem from larger number of filaments in the colonies from the Atlantic compared with those from the Red Sea (Basu & Shaked, 2018; Taboada et al., 2010). Based on these experiments and observations, we draw the threshold of dust that Red Sea puff-shaped colonies can bear and stay afloat at few hundred nanograms.

3.1.2. Effect of Dust on Colony Sinking Velocity

Initial sinking velocities for individual colonies were examined three times: without any dust, with medium dust load (20–1,400 ng colony^{-1}), and with high dust load (330–4,400 ng colony^{-1}). Experiments were repeated on

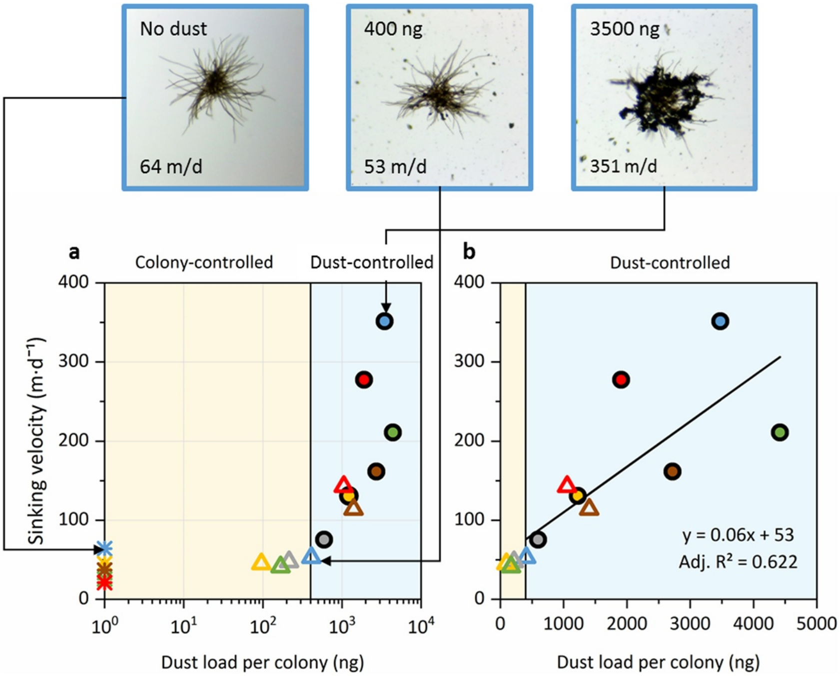


Figure 2. Effect of dust load on sinking velocities of Rea Sea *T. thiebautii* colonies. (a) Sinking velocities of six individual colonies, each measured repeatedly with increasing dust loads and labeled with a distinct color. Sinking velocities of particle-free colonies are noted by stars, colonies with medium dust load by triangles and colonies with high dust load by circles. Two regions were identified: colony-controlled area (yellow shaded) and dust-controlled area (blue shaded). Images above show the increasing dust loads of a single colony (blue-labeled). (b) Zoom-in on the dust-controlled zone, where sinking velocity increased linearly with dust load, at a slope (K) that matched theoretical calculations (see text).

five different days, obtaining 75 data pairs of dust loads and sinking velocities (see Supporting Information S1: Table S2). As before, colonies were imaged prior to, and after, each step to track their actual dust loads. Data from two representative days (October 18th and 20th 2020) with six individual colonies show that moderate dust load of 100–400 ng did not affect the colony's sinking velocity, which remained at 40–50 m·d^{-1} (Figure 2a). The initial colony sinking velocities at these low dust loads were probably controlled by colony size, colony composition (i.e., carbohydrate content) and gas vesicles but not by dust (Held et al., 2022; Walsby, 1992), a region which we term "colony-controlled" (Figure 2, yellow area). This region is typified by the lack of effect of dust on the initial colony sinking velocity and is in-line with our other observations from the sedimentation chambers after 15 min (Figure 1). Combined with field observations (Figure 1a), our results suggest that Red Sea colonies can maintain their buoyancy when interacting with several hundred nanograms of dust.

Further dust addition (1–4 μg per colony) shifted the measured sinking velocities into a dust-controlled region (Figure 2, blue area). In this region, sinking velocities increased linearly with the colony's dust load (Figure 2b). A linear relationship is expected based on theoretical considerations (Stoke's law) and direct sinking velocity measurements of size-specific ballasted aggregates (Engel et al., 2009; Iversen & Ploug, 2010). However, according to Stoke's law, sinking velocity is impacted by both, aggregate size and density (e.g., Laurenceau-Cornec et al., 2020). In our case, the colony size remained unchanged for all dust loads since it was centered within the colony core (as confirmed by microscopic observations). Taking into consideration the colony volume and density and the centered dust we derived a linear relationship between dust load and colony sinking velocity (Equation 1), that should apply for the blue region (see methods and Supporting Information S1: Text S1 and S2). This theoretical calculation predicted a slope (K) of 0.02–0.06 m·d^{-1} ng^{-1}, implying that 100 ng dust will increase the colony sinking velocity by 2–6 m per day. Our experimental data yielded a slope (K) of 0.06 m·d^{-1} ng^{-1} (Figure 2b) very similar to these theoretical predictions and thus supports our experimental approach. The match between experiments and predictions holds for dust-loaded colonies but not for dust-free colonies. Our measured sinking velocities of particle-free colonies (40–55 m·d^{-1}, Figure 2) exceed their predicted sinking velocities

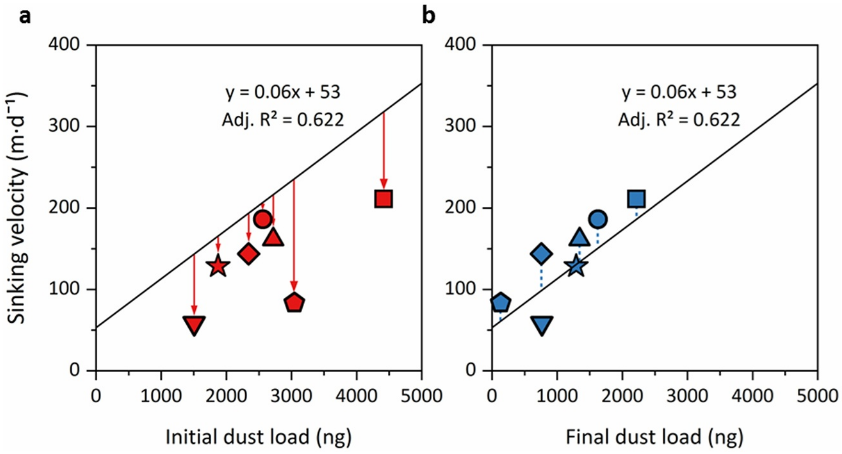


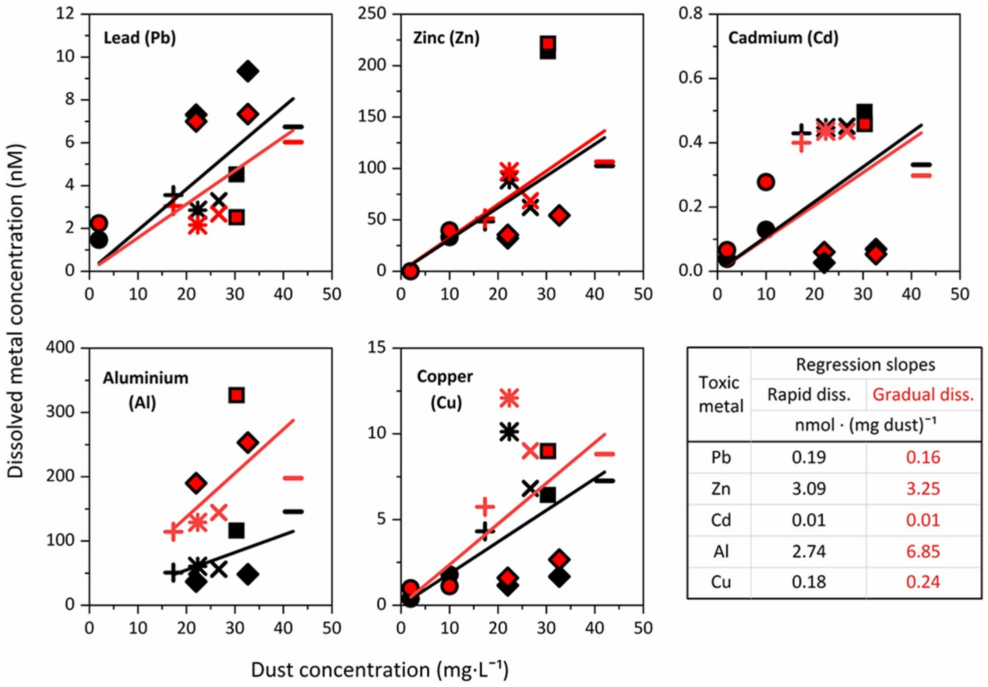
Figure 3. Effect of dust loss on colony sinking velocity. Measured sinking velocities of seven representative colonies (shown as different symbols) plotted against their initial (a) and final (b) dust loads. The equation (black line) is the linear relationship established in Figure 2b. Arrows and dash lines indicate the mismatch of measured sinking velocities and expected velocities calculated from initial and final dust loads, respectively. See Supporting Information S1: Figure S3 for additional colonies.

(0–9 m·d^{-1}, see Supporting Information S1: Table S5). Yet, this mismatch may be explained by *Trichodesmium's* ability to modify their density (Romans et al., 1994; Villareal & Carpenter, 1990).

The sinking velocities measured (20–60 m·d^{-1}) for particle-free colonies (Figure 2) compare well with those of Walsby (1978), who experimentally observed maximal sinking velocities of 60 m·d^{-1} for natural *Trichodesmium thiebautii* from the Sargasso and Caribbean Sea. The vertical motion of *Trichodesmium* has been reported early on (Kromkamp et al., 1992; Villareal & Carpenter, 2003), and draws large interest in terms of carbon export to depth (Bonnet et al., 2023), and fueling of the deep ocean with fixed nitrogen (Benavides et al., 2022). Such vertical migration was hypothesized to provide an ecological advantage to *Trichodesmium* and enable it to mine phosphorus from the nutricline (Karl et al., 1992; White et al., 2006). Sinking of *Trichodesmium* colonies can occur through gravitational sinking or downwelling events (Guidi et al., 2012), both of which can further be accelerated by mineral ballasting (Pabortsava et al., 2017) or sudden autocatalytic cell death in response to nutrient limitation (Berman-Frank et al., 2004). Our study is the first to experimentally quantify the effect of dust on the colony's sinking velocity, and our findings are conform to theoretical predictions, modeling data, as well as in situ observations (Laurenceau-Cornec et al., 2020; Walsby, 1978; White et al., 2006). To conclude, our experiments show that *Trichodesmium* colonies can control their buoyancy even when loaded with up to 300–400 ng dust and that collection of 1 μg dust will increase their sinking velocity by ~60 m·d^{-1}. Upon demise, when *Trichodesmium's* gas vesicles collapse, all dust loads can cause a ballast effect and increase the export of particulate organic carbon (POC) to depth.

3.1.3. Effect of Dust Loss on Colony Sinking Velocity

During sedimentation experiments a significant loss of particles from most colonies (42 out of 50 total data pairs) was observed, especially from the heavily loaded ones. Comparing colony images taken prior to and after the experiments, a loss of 10 ng - 3 μg dust per colony was calculated (see Supporting Information S1: Table S6). This massive loss of dust is expected to decrease the sinking velocity of colonies if the loss occurred in early stages of the experiment. Seeking to illustrate this effect, several representative colonies were plotted in Figure 3 (see the selection criterion in Supporting Information S1: Text S3) and compared to the linear relationship established in Figure 2b ($y = 0.06$ m·d^{-1} ng^{-1} x dust weight (ng) + 53 m·d^{-1}). All these colonies plot below their expected sinking velocities noted by the black line, indicating that dust was lost during the experiment and decreased their sinking velocities (Figure 3a). Replotting the measured sinking velocities of these colonies against their final dust loads (Figure 3b), yield values that are nearer to the line. Thus, it seems that these colonies were sinking at velocities that match the final dust loads, probably since this loss occurred at the beginning of the experiment.



Toxic metal	Regression slopes Rapid diss.	Gradual diss.
	nmol · (mg dust)$^{-1}$	
Pb	0.19	0.16
Zn	3.09	3.25
Cd	0.01	0.01
Al	2.74	6.85
Cu	0.18	0.24

Figure 4. Compilation of dust dissolution experiments conducted in seawater using different dust samples and concentrations. The data set combines new measurements (circles) and published data from Mackey et al. (2015) and includes seven dust samples plotted as different symbols. Metal release kinetics is presented by two categories - rapidly released metals (black, up to 6 hr) and gradually released metals (red, up to 7 days). Regression slopes linking dust and dissolved metal concentrations are plotted and summarized in the table next to the graph. See Supporting Information S1: Figure S8 for additional elements.

Such analysis, made possible by the relationship established in this study, revealed that dust loss can decrease the colony sinking velocity in a predictable manner.

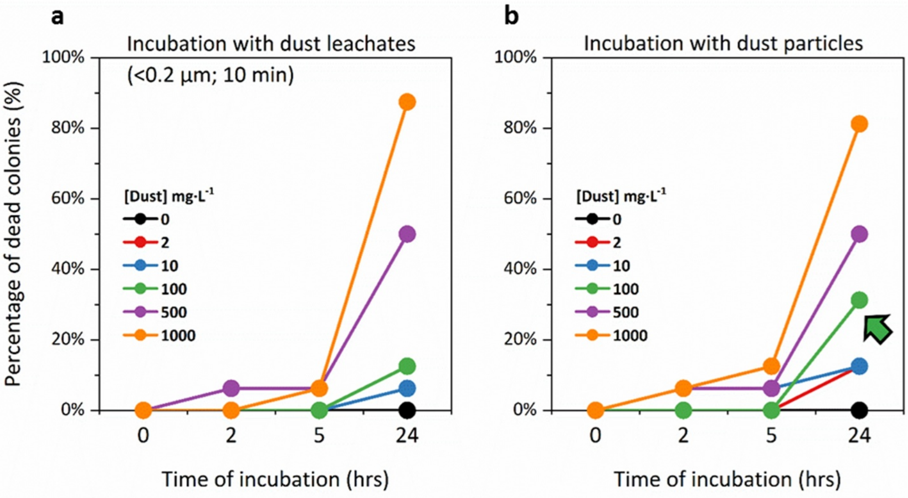
3.2. Toxic Effects of Dust on *Trichodesmium*

Dust and other aerosols contain an array of toxic elements (Bozlaker et al., 2013). Upon dust deposition on the surface ocean, some elements are rapidly released and may induce toxicity to positively buoyant *Trichodesmium* blooms that accumulate at the surface. Seeking to evaluate the toxicity of dust to *Trichodesmium* blooms, the fraction of rapidly released toxic metals was measured and the impact of dust leachate on *Trichodesmium* mortality was observed. In addition, colonies that concentrate dust may also experience a continuous flux of toxic metals that are gradually released from the centered particles. The gradual release of metals was measured and the mortality of dust-loaded colonies was examined.

3.2.1. Kinetics of Toxic Metal Release From Dust

Toxic metal release to seawater was measured at two dust concentrations and data was gathered according to time, differentiating between rapidly (10 min-6 hr) and gradually (12 hr-7 d) released elements. To contextualize our data, we included additional dissolution measurements conducted by Mackey et al. (2015) resulting in a dissolution data set composed of seven different dust samples collected from the Gulf of Aqaba over several years (Figure 4, see Supporting Information S1: Table S7 for additional elements). To enable easy extrapolation to natural conditions, concentrations of dissolved metal released from the different dust samples were plotted against the concentrations of dust used in the experiments. In general, higher dissolved metals were recorded at higher dust concentrations and a linear correlation can be fitted to the data (Figure 4).

Since *Trichodesmium's* exposure to dust depends on the interaction time, special attention was paid to the timing and release mode of each metal, following the Mackey et al. (2015) scheme. Concentrations of zinc (Zn) and cadmium (Cd) remained constant with time (gradual = rapid, Figure 4) and hence were considered rapidly



c Calculated toxic metal release from dust

Dust concn. (mg·L^{-1})	Rapid release in dust-leachates (nM)					Gradual release (nM)	
	Pb	Zn	Cd	Al	Cu	Al*	Cu*
1000	190	3090	10	2740	180	4110	60
500	95	1545	5	1370	90	2055	30
100	19	309	1	274	18	411	6
10	1.9	31	0.1	27	1.8	41	0.6
2	0.4	6	0.0	5	0.4	8	0.1

* represents additional release during incubation

Figure 5. Impact of dust on mortality of Red Sea *Trichodesmium* colonies and estimated toxic metals released during incubations. Mortality of natural colonies incubated for 24 hr with increasing concentrations of (a) dust leachate and (b) whole dust. (c). Calculated metal release from dust during the mortality assays based on the regression slopes obtained in Figure 4. Data was compiled from 2 different experiments. The dust leachate was filtered within 10 min of dust suspension in seawater to represent rapidly released metals, while whole dust provided also gradually released metals. The toxicity of dust leachate and whole dust was comparable at high concentrations, but as indicated by the green arrow, at 100 mg L^{-1} dust, the mortality was higher with whole dust.

released elements. On the other hand, aluminum (Al) and copper (Cu) accumulated with dissolution time (gradual > rapid, Figure 4), and were considered gradually released elements. Lead (Pb) concentration dropped slightly with time (gradual < rapid, Figure 4), reflecting its tendency to adsorb onto particles and surfaces (Bruland et al., 2013). Based on these linear slopes and release mode (rapid vs. gradual), the "cocktail" of toxic elements released during dust deposition events or within the colony center can be evaluated and linked to the incubation studies with *Trichodesmium*.

3.2.2. Dust Toxicity to *Trichodesmium*—Fractions and Doses

To assess dust toxicity to *Trichodesmium*, ~180 freshly collected natural colonies were incubated with increasing dust concentrations for 24 hr and mortality was assessed visually based on colony integrity and filament degradation (see Supporting Information S1: Figure S4). To distinguish between the toxic effects of rapidly and gradually released metals, colonies were exposed to dust leachate and raw dust, respectively (where the leachate was obtained after 10 min from dust addition to seawater).

Incubating *Trichodesmium* with 2 and 10 mg·L^{-1} dust resulted in negligible mortality of only one or two of the 16 colonies dead (red and blue lines in Figures 5a and 5b). These dust loads are within the range reported for natural dust storms (<10 mg·L^{-1}, Ren et al., 2011; Zhang et al., 2019), and hence dust load from such storms are not predicted to induce *Trichodesmium* mortality. Low mortality (13%) was observed in colonies incubated with 100 mg·L^{-1} dust leachate, far below the LC50 toxicity threshold, which is the lethal concentration that results in death of 50% of the colonies (Echeveste et al., 2012). At higher dust concentrations of 500 and 1,000 mg·L^{-1}, significant mortality was observed, ranging from 50% to 90% of the colonies (purple and orange lines in

Figures 5a and 5b), indicative of acute toxicity. Based on these incubations, we conservatively set the LC50 toxicity threshold at 500 mg·L^{-1} (although it may occur anywhere above 100 mg·L^{-1}).

Overall, the mortality of *Trichodesmium* incubated with dust leachates (Figure 5a) was almost as high as in the incubation with dust particles (Figure 5b). This implies that metals released from dust during 10 min are the key contributors to their toxicity to *Trichodesmium*. Utilizing the linear fit from Figure 4, toxic metal concentrations in each incubation can be estimated (Figure 5c). For example, in the incubation with 500 mg·L^{-1} dust, resulting in 50% mortality, *Trichodesmium* is expected to experience 5 nM Cd, 95 nM Pb, 90 nM Cu, and >1 μM of Zn and Al (Figure 5c). Interestingly, negligible mortality occurred in the 100 mg·L^{-1} dust leachate incubation, inducing conditions where 1 nM Cd, ∼20 nM Pb and Cu, and ∼300 nM of Zn and Al were predicted (Figures 5b and 5c). Given the absence of literature data on *Trichodesmium*'s response to a cocktail of toxic metals, it remains inconclusive whether these levels were sub-lethal or *Trichodesmium* was simply capable of detoxifying these metals. Typically, toxicity thresholds (e.g., effective concentration 50% (EC50s) or lethal concentration 50% (LC50s) are obtained for a single metal, varying amongst phytoplankton types and sizes (Echeveste et al., 2012; Paytan et al., 2009; Yang et al., 2019). To provide context, Cd and Pb toxicity thresholds (LC50s) for natural phytoplankton from different ocean basins were reported to range from 2 to 4,000 nM for Cd, and 100–2,000 nM for Pb (Echeveste et al., 2012).

However, a more detailed look at the data does reveal subtle changes in the mortality of colonies, which were incubated with low (2–100 mg·L^{-1}) dust leachate compared to the whole dust (as noted by the green arrow in Figure 5 and Figure S7 in Supporting Information S1). At these low dust concentrations (2, 10 and 100 mg·L^{-1}), which were generally not toxic, the presence of particles resulted in added mortality. We propose that this added mortality has originated from gradually released metals, such as Al and Cu (Figure 5c). In a parallel set of experiments, we tested the mortality of colonies, which were incubated with increasing Cu concentrations, obtaining 30% and 50% mortality at 5 and 10 nM Cu, respectively (see Supporting Information S1: Figure S5). The estimated gradual release of 0.1–6 nM Cu (Figure 5c) may hereby explain the elevated mortality in the whole dust incubation, especially when considering the high levels of Al.

Regarding the toxicity of metals in dust-centering colonies, it appears that Zn and Cd are not a major concern, as these elements are released from dust before they interact with the colonies. Pb is rapidly released from dust, whilst it can be toxic to colonies, due to reabsorption onto particles and cells (Mackey et al., 2015). But the gradually released elements Al and Cu may cause toxicity to colonies that center dust. As dust is confined within the colony core and the diffusion to the surrounding water is limited, the colony, or better its core volume, should be considered as the relevant volume for metal release. Given ∼1 μL colony volume, dust loads of 0.2–1 μg yield effective dust concentration of 200–1,000 mg·L^{-1} (see Supporting Information S1: Figure S9). At these high dust concentrations, high exposure to gradually released Al and Cu is expected (Figure 5c). The exposure to these metals may be even larger when considering the volume of the colony core, where dissolution occurs, and not the entire colony volume. Nonetheless, colonies that accumulated even higher dust loads (1–10 μg) showed no signs of mortality during incubations that lasted 24 hr (see Supporting Information S1: Figure S10). The survival of colonies with an effective dust load of over 1,000 mg·L^{-1} and projected high Cu and Al fluxes (Figure 5c) is intriguing. These observations call for further research measuring metal fluxes within colonies and exploring possible detoxification and physiological defense mechanisms. Such mechanisms may include metal binding by extracellular polymeric substances (EPS) and specific ligands (Gledhill et al., 2019) and metal excretion through efflux proteins (Hewson et al., 2009).

3.2.3. Selective Removal of Cu Minerals

Hypothesizing that colonies may try to reduce toxicity through the removal of particles, natural colonies were incubated with Cu-containing minerals (malachite) for 24 hr. To ensure optimal colony-mineral interactions, the Cu minerals were mixed with Fe minerals (hematite), which are typically preferred by *Trichodesmium*. All colonies interacted strongly with particles throughout the incubation and showed strong preference for the Fe-minerals. Only few colonies contained Cu-minerals, but these were present even at 24 hr (Figure 6). The finding of Cu minerals on colonies at the end of the incubation does not support our hypothesis and there is currently no evidence to support the selective removal of toxic minerals.

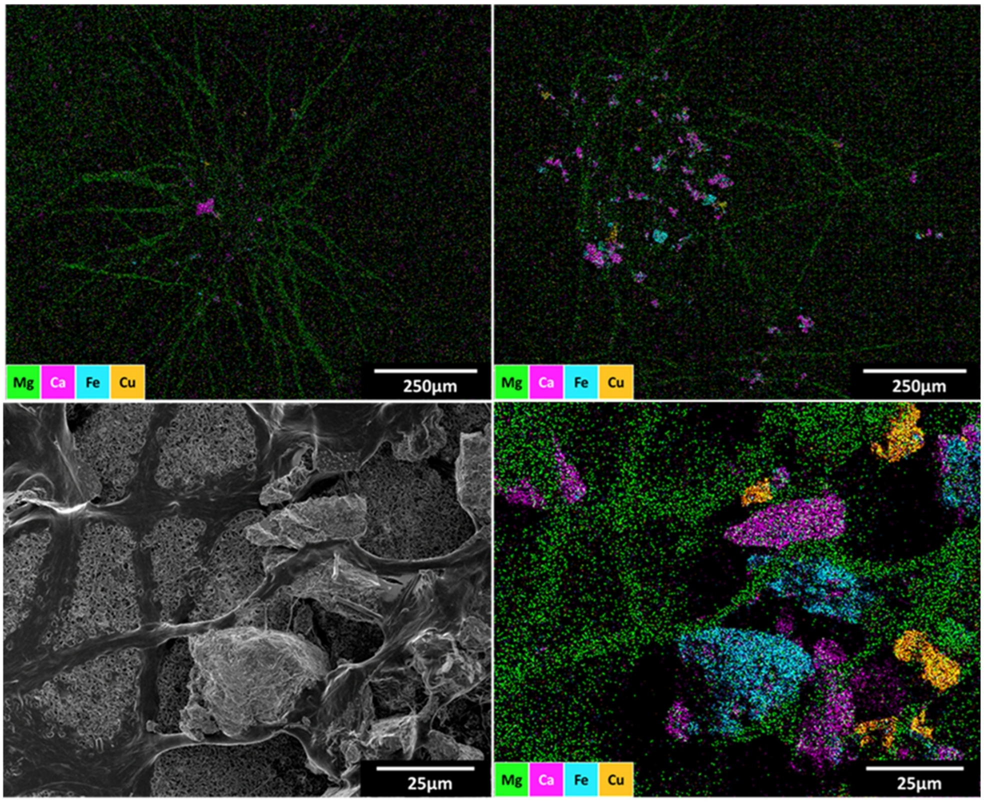


Figure 6. SEM-EDX images of natural *Trichodesmium* colonies incubated with Cu-minerals (malachite) and Fe-minerals (hematite). Probing the ability of *Trichodesmium* to distinguish and selectively remove toxic particles, colonies were incubated with malachite and hematite up to 24 hr. Several colonies were imaged at different magnification (scale bars within images), showing the presence of both minerals throughout the incubation (Cu—yellow, Fe—blue). *Trichodesmium* was imaged through its magnesium content (green) and the malachite sample also contained calcium (Ca) minerals (pink). See Supporting Information S1: Figures S12–S15 for additional elemental maps.

4. Summary

Having studied the potential negative effects of dust on natural *Trichodesmium* colonies, we predict that in a typical open-ocean setting, the potential benefit of dust as a nutrient source outweighs the risks of buoyancy loss and toxification. In the Gulf of Aqaba, puff-shaped *T. thiebautii* colonies collected in situ were usually observed to contain less than 200 ng of dust per colony, which is below the threshold where sinking velocity becomes dust-controlled (Figure 1) and is insufficient to induce toxicity through metal release (Figure 5). In other environments (e.g., coastal seas, Mackey et al., 2012), however, *Trichodesmium* may encounter more toxic aerosols and the concepts laid here may facilitate the evaluation of those risks. With regards to buoyancy, accelerated sinking velocities due to interactions with dust may be significant to C export, and may help explain recent measurements of active N_2 fixation by *Trichodesmium* at 1,000 m (Benavides et al., 2022). If indeed colonies can modulate their particle load, the dust-induced sinking may benefit *Trichodesmium* and expand its ecological niche.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

Data generated for this study were uploaded as supplementary materials. Hydrographic data at the time of colony sampling in this study are available at the IUI's website (http://www.meteo-tech.co.il/EilatYam_data/ey_data.asp) (National monitoring program [Dataset], 2024). All python codes for sinking velocity can be found in Github (https://github.com/Zhanzhu1110/Trichobuoyancy.git) and in Zenodo (https://zenodo.org/records/10290901;

DOI:10.5281/zenodo.10290901) (Wang et al., 2023). Data of metal release (dust concentrations = 17–42 mg·L^{-1}) are available from Mackey et al. (2015), and a complete supplementary data file is also provided herein for ease of access.

Acknowledgments

We extend our sincere gratitude to Murielle Dray (IUI) and Emanuel Sestieri (IUI) for their invaluable assistance during this study. We appreciate the Mineral collection at the National Natural History Collections at the Hebrew University for donating the mineral specimens (hematite) used in this work. Siyuan Wang thanks Prof. Angelicque E. White for her insightful suggestions regarding the model of sinking velocity and to Antonio Colussi and Dr. Lina Sakhneny for their contributions to colony collection and toxicity assays. This study was funded by ISF-NSFC joint research program (Grant 2398/18), ISF (260/21) and German-Israeli Foundation for Scientific Research and Development (Grant 1349). Siyuan Wang acknowledges CSC-HUJI doctoral fellowship and Futing Zhang acknowledges PBC Postdoctoral fellowship.

References

Anderson, O. R. (1977). Fine structure of a marine Ameba associated with a blue-green Alga in the Sargasso sea. *Journal of Protozoology*, *24*(3), 370–376. https://doi.org/10.1017/cbo9780511600586.003

Basu, S., Gledhill, M., de Beer, D., Prabhu Matondkar, S. G., & Shaked, Y. (2019). Colonies of marine cyanobacteria *Trichodesmium* interact with associated bacteria to acquire iron from dust. *Communications Biology*, *2*(1), 1–8. https://doi.org/10.1038/s42003-019-0534-z

Basu, S., & Shaked, Y. (2018). Mineral iron utilization by natural and cultured *Trichodesmium* and associated bacteria. *Limnology & Oceanography*, *63*(6), 2307–2320. https://doi.org/10.1002/lno.10939

Benaltabet, T., Lapid, G., & Torfstein, A. (2022). Dissolved aluminium dynamics in response to dust storms, wet deposition, and sediment resuspension in the Gulf of Aqaba, northern Red Sea. *Geochimica et Cosmochimica Acta*, *335*, 137–154. https://doi.org/10.1016/j.gca.2022.08.029

Benavides, M., Bonnet, S., Le Moigne, F. A. C., Armin, G., Inomura, K., Hallstrøm, S., et al. (2022). Sinking *Trichodesmium* fixes nitrogen in the dark ocean. *ISME Journal*, *16*(10), 2398–2405. https://doi.org/10.1038/s41396-022-01289-6

Berman-Frank, I., Bidle, K. D., Haramaty, L., & Falkowski, P. G. (2004). The demise of the marine cyanobacterium, *Trichodesmium* spp., via an autocatalyzed cell death pathway. *Limnology & Oceanography*, *49*(4 I), 997–1005. https://doi.org/10.4319/lo.2004.49.4.0997

Bif, M. B., & Yunes, J. S. (2017). Distribution of the marine cyanobacteria *Trichodesmium* and their association with iron-rich particles in the South Atlantic Ocean. *Aquatic Microbial Ecology*, *78*(2), 107–119. https://doi.org/10.3354/ame01810

Bonnet, S., Benavides, M., Le Moigne, F. A. C., Camps, M., Torremocha, A., Grosso, O., et al. (2023). Diazotrophs are overlooked contributors to carbon and nitrogen export to the deep ocean. *ISME Journal*, *17*(1), 47–58. https://doi.org/10.1038/s41396-022-01319-3

Bozlaker, A., Prospero, J. M., Fraser, M. P., & Chellam, S. (2013). Quantifying the contribution of long-range saharan dust transport on particulate matter concentrations in Houston, Texas, using detailed elemental analysis. *Environmental Science and Technology*, *47*(18), 10179–10187. https://doi.org/10.1021/es4015663

Bruland, K. W., Middag, R., & Lohan, M. C. (2013). Controls of trace metals in seawater. *Treatise on Geochemistry: Second Edition*, *8*, 19–51. https://doi.org/10.1016/B978-0-08-095975-7.00602-1

Capone, D. G., Zehr, J. P., Paerl, H. W., Bergman, B., & Carpenter, E. J. (1997). *Trichodesmium*, a globally significant marine cyanobacterium. *Science*, *276*(5316), 1221–1229. https://doi.org/10.1126/science.276.5316.1221

Cerdan-Garcia, E., Baylay, A., Polyviou, D., Woodward, E. M. S., Wrightson, L., Mahaffey, C., et al. (2022). Transcriptional responses of *Trichodesmium* to natural inverse gradients of Fe and P availability. *ISME Journal*, *16*(4), 1055–1064. https://doi.org/10.1038/s41396-021-01151-1

Chen, Y., Tovar-Sanchez, A., Siefert, R. L., Sañudo-Wilhelmy, S. A., & Zhuang, G. (2011). Luxury uptake of aerosol iron by *Trichodesmium* in the western tropical North Atlantic. *Geophysical Research Letters*, *38*(18). https://doi.org/10.1029/2011GL048972

Echeveste, P., Agustí, S., & Tovar-Sánchez, A. (2012). Toxic thresholds of cadmium and lead to oceanic phytoplankton: Cell size and ocean basin-dependent effects. *Environmental Toxicology and Chemistry*, *31*(8), 1887–1894. https://doi.org/10.1002/etc.1893

Eichner, M., Inomura, K., Pierella Karlusich, J. J., & Shaked, Y. (2023). Better together? Lessons on sociality from *Trichodesmium*. *Trends in Microbiology*, *31*(10), 1072–1084. https://doi.org/10.1016/j.tim.2023.05.001

Engel, A., Szlosek, J., Abramson, L., Liu, Z., & Lee, C. (2009). Investigating the effect of ballasting by $CaCO_3$ in *Emiliania huxleyi*: I. Formation, settling velocities and physical properties of aggregates. *Deep-Sea Research Part II Topical Studies in Oceanography*, *56*(18), 1396–1407. https://doi.org/10.1016/j.dsr2.2008.11.027

Frischkorn, K. R., Haley, S. T., & Dyhrman, S. T. (2018). Coordinated gene expression between *Trichodesmium* and its microbiome over day-night cycles in the north Pacific subtropical Gyre. *ISME Journal*, *12*(4), 997–1007. https://doi.org/10.1038/s41396-017-0041-5

Gledhill, M., Basu, S., & Shaked, Y. (2019). Metallophores associated with: *Trichodesmium erythraeum* colonies from the Gulf of Aqaba. *Metallomics*, *11*(9), 1547–1557. https://doi.org/10.1039/c9mt00121b

Guidi, L., Calil, P. H. R., Duhamel, S., Björkman, K. M., Doney, S. C., Jackson, G. A., et al. (2012). Does eddy-eddy interaction control surface phytoplankton distribution and carbon export in the North Pacific Subtropical Gyre? *Journal of Geophysical Research: Biogeosciences*, *117*(2), 1–12. https://doi.org/10.1029/2012JG001984

Guo, C., Zhou, Y., Zhou, H., Su, C., & Kong, L. (2022). Aerosol nutrients and their biological influence on the northwest Pacific ocean (NWPO) and its Marginal seas. *Biology*, *11*(6), 1–18. https://doi.org/10.3390/biology11060842

Held, N. A., Sutherland, K. M., Webb, E. A., McIlvin, M. R., Cohen, N. R., Devaux, A. J., et al. (2021). Mechanisms and heterogeneity of *in situ* mineral processing by the marine nitrogen fixer *Trichodesmium* revealed by single-colony metaproteomics. *ISME Communications*, *1*(1), 1–9. https://doi.org/10.1038/s43705-021-00034-y

Held, N. A., Waterbury, J. B., Webb, E. A., Kellogg, R. M., McIlvin, M. R., Jakuba, M., et al. (2022). Dynamic diel proteome and daytime nitrogenase activity supports buoyancy in the cyanobacterium *Trichodesmium*. *Nature Microbiology*, *7*(2), 300–311. https://doi.org/10.1038/s41564-021-01028-1

Held, N. A., Webb, E. A., McIlvin, M. M., Hutchins, D. A., Cohen, N. R., Moran, D. M., et al. (2020). Co-occurrence of Fe and P stress in natural populations of the marine diazotroph *Trichodesmium*. *Biogeosciences*, *17*(9), 2537–2551. https://doi.org/10.5194/bg-17-2537-2020

Hewson, I., Poretsky, R. S., Dyhrman, S. T., Zielinski, B., White, A. E., Tripp, H. J., et al. (2009). Microbial community gene expression within colonies of the diazotroph, *Trichodesmium*, from the Southwest Pacific Ocean. *ISME Journal*, *3*(11), 1286–1300. https://doi.org/10.1038/ismej.2009.75

Iversen, M. H., & Ploug, H. (2010). Ballast minerals and the sinking carbon flux in the ocean: Carbon-specific respiration rates and sinking velocity of marine snow aggregates. *Biogeosciences*, *7*(9), 2613–2624. https://doi.org/10.5194/bg-7-2613-2010

Janson, S., Siddiqui, P. J. A., Walsby, A. E., Romans, K. M., Carpenter, E. J., & Bergman, B. (1995). Cytomorphological characterization of the planktonic diazotrophic cyanobacteria *trichodesmium* SPP. From the INDIAN ocean and caribbean and sargasso SEAS1. *Journal of Phycology*, *31*(3), 463–477. https://doi.org/10.1111/j.0022-3646.1995.00463.x

Karl, D. M., Letelier, R., Hebel, D. V., Bird, D. F., Winn, C. D., & Carpenter, J. G. (1992). *Trichodesmium* blooms and new nitrogen in the North Pacific gyre. In E. J. Capone & D. G. Rueter (Eds.), *Marine pelagic cyanobacteria* (pp. 219–237). Springer. https://doi.org/10.1007/978-94-015-7977-3_14

Kessler, N., Armoza-Zvuloni, R., Wang, S., Basu, S., Weber, P. K., Stuart, R. K., & Shaked, Y. (2020). Selective collection of iron-rich dust particles by natural *Trichodesmium* colonies. *ISME Journal*, *14*(1), 91–103. https://doi.org/10.1038/s41396-019-0505-x

Kessler, N., Kraemer, S. M., Shaked, Y., & Schenkeveld, W. D. C. (2020). Investigation of siderophore-promoted and reductive dissolution of dust in marine microenvironments such as *Trichodesmium* colonies. *Frontiers in Marine Science*, *7*(March), 1–15. https://doi.org/10.3389/fmars.2020.00045

Koedooder, C., Landou, E., Zhang, F., Wang, S., Basu, S., Berman-Frank, I., et al. (2022). Metagenomes of Red Sea subpopulations challenge the use of marker genes and morphology to assess *Trichodesmium* diversity. *Frontiers in Microbiology*, *13*(May). https://doi.org/10.3389/fmicb.2022.879970

Krisch, S., Hopwood, M. J., Roig, S., Gerringa, L. J. A., Middag, R., Rutgers van der Loeff, M. M., et al. (2022). Arctic – Atlantic exchange of the dissolved micronutrients iron, Manganese, Cobalt, Nickel, copper and zinc with a focus on fram strait. *Global Biogeochemical Cycles*, *36*(5). https://doi.org/10.1029/2021GB007191

Kromkamp, J., & Walsby, A. E. (1990). A computer model of buoyancy and vertical migration in cyanobacteria. *Journal of Plankton Research*, *12*(1), 161–183. https://doi.org/10.1093/plankt/12.1.161

Kromkamp, J., Walsby, A. E., & Carpenter, J. G. (1992). Buoyancy regulation and vertical migration of *Trichodesmium*: A computer-model prediction. In E. J. Capone & D. G. Rueter (Eds.), *Marine pelagic cyanobacteria: Trichodesmium and other diazotrophs* (pp. 239–248). Springer. https://doi.org/10.1007/978-94-015-7977-3_15

Laurenceau-Cornec, E. C., Le Moigne, F. A. C., Gallinari, M., Moriceau, B., Toullec, J., Iversen, M. H., et al. (2020). New guidelines for the application of Stokes' models to the sinking velocity of marine aggregates. *Limnology & Oceanography*, *65*(6), 1264–1285. https://doi.org/10.1002/lno.11388

Lee, M. D., Walworth, N. G., McParland, E. L., Fu, F. X., Mincer, T. J., Levine, N. M., et al. (2017). The *Trichodesmium* consortium: Conserved heterotrophic co-occurrence and genomic signatures of potential interactions. *ISME Journal*, *11*(8), 1813–1824. https://doi.org/10.1038/ismej.2017.49

Lundgren, P., Janson, S., Jonasson, S., Singer, A., & Bergman, B. (2005). Unveiling of novel radiations within *Trichodesmium* cluster by hetR gene sequence analysis. *Applied and Environmental Microbiology*, *71*(1), 190–196. https://doi.org/10.1128/AEM.71.1.190-196.2005

Mackey, K. R. M., Buck, K. N., Casey, J. R., Cid, A., Lomas, M. W., Sohrin, Y., & Paytan, A. (2012). Phytoplankton responses to atmospheric metal deposition in the coastal and open-ocean Sargasso Sea. *Frontiers in Microbiology*, *3*(OCT), 1–15. https://doi.org/10.3389/fmicb.2012.00359

Mackey, K. R. M., Chien, C. T., Post, A. F., Saito, M. A., & Paytan, A. (2015). Rapid and gradual modes of aerosol trace metal dissolution in seawater. *Frontiers in Microbiology*, *6*(JAN), 1–11. https://doi.org/10.3389/fmicb.2014.00794

Mahowald, N. M., Hamilton, D. S., Mackey, K. R. M., Moore, J. K., Baker, A. R., Scanza, R. A., & Zhang, Y. (2018). Aerosol trace metal leaching and impacts on marine microorganisms. *Nature Communications*, *9*(1), 2614. https://doi.org/10.1038/s41467-018-04970-7

McConnell, C. L., Highwood, E. J., Coe, H., Formenti, P., Anderson, B., Osborne, S., et al. (2008). Seasonal variations of the physical and optical characteristics of saharan dust: Results from the dust outflow and deposition to the ocean (DODO) experiment. *Journal of Geophysical Research*, *113*(D14), 1–19. https://doi.org/10.1029/2007JD009606

Mills, M. M., Ridame, C., Davey, M., La Roche, J., & Geider, R. J. (2004). Iron and phosphorus co-limit nitrogen fixation in the eastern tropical North Atlantic. *Nature*, *429*(6989), 292–294. https://doi.org/10.1038/nature03632

National monitoring program [Dataset]. (2024). National monitoring program [Dataset]. *NMP*. Retrieved from http://www.meteo-tech.co.il/EilatYam_data/ey_data.asp

Pabortsava, K., Lampitt, R. S., Benson, J., Crowe, C., McLachlan, R., Le Moigne, F. A. C., et al. (2017). Carbon sequestration in the deep Atlantic enhanced by Saharan dust. *Nature Geoscience*, *10*(3), 189–194. https://doi.org/10.1038/ngeo2899

Paytan, A., Mackey, K. R. M., Chen, Y., Lima, I. D., Doney, S. C., Mahowald, N., et al. (2009). Toxicity of atmospheric aerosols on marine phytoplankton. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(12), 4601–4605. https://doi.org/10.1073/pnas.0811486106

Pierella Karlusich, J. J., Pelletier, E., Lombard, F., Carsique, M., Dvorak, E., Colin, S., et al. (2021). Global distribution patterns of marine nitrogen-fixers by imaging and molecular methods. *Nature Communications*, *12*(1), 1–18. https://doi.org/10.1038/s41467-021-24299-y

Polyviou, D., Baylay, A. J., Hitchcock, A., Robidart, J., Moore, C. M., & Bibby, T. S. (2018). Desert dust as a source of iron to the globally important diazotroph *Trichodesmium*. *Frontiers in Microbiology*, *8*(JAN), 1–12. https://doi.org/10.3389/fmicb.2017.02683

Post, A. F., Dedej, Z., Gottlieb, R., Li, H., Thomas, D. N., El-Absawi, M., et al. (2002). Spatial and temporal distribution of *Trichodesmium* spp. in the stratified Gulf of Aqaba, Red Sea. *Marine Ecology Progress Series*, *239*(May 2014), 241–250. https://doi.org/10.3354/meps239241

Rapp, I., Schlosser, C., Rusiecka, D., Gledhill, M., & Achterberg, E. P. (2017). Automated preconcentration of Fe, Zn, Cu, Ni, Cd, Pb, Co, and Mn in seawater with analysis using high-resolution sector field inductively-coupled plasma mass spectrometry. *Analytica Chimica Acta*, *976*, 1–13. https://doi.org/10.1016/j.aca.2017.05.008

Ren, J. L., Zhang, G. L., Zhang, J., Shi, J. H., Liu, S. M., Li, F. M., et al. (2011). Distribution of dissolved aluminum in the Southern Yellow Sea: Influences of a dust storm and the spring bloom. *Marine Chemistry*, *125*(1–4), 69–81. https://doi.org/10.1016/j.marchem.2011.02.004

Romans, K. M., Carpenter, E. J., & Bergman, B. (1994). Buoyancy regulation in the colonial diazotrophic cyanobacterium *Trichodesmium tenue*: Ultrastructure and storage of carbohydrate, polyphosphate, and nitrogen. *Journal of Phycology*, *30*(6), 935–942. https://doi.org/10.1111/j.0022-3646.1994.00935.x

Rouco, M., Haley, S. T., & Dyhrman, S. T. (2016). Microbial diversity within the *Trichodesmium* holobiont. *Environmental Microbiology*, *18*(12), 5151–5160. https://doi.org/10.1111/1462-2920.13513

Rouco, M., Joy-Warren, H., McGillicuddy, D. J., Waterbury, J. B., & Dyhrman, S. T. (2014). *Trichodesmium* sp. clade distributions in the western north atlantic ocean. *Limnology & Oceanography*, *59*(6), 1899–1909. https://doi.org/10.4319/lo.2014.59.6.1899

Rubin, M., Berman-Frank, I., & Shaked, Y. (2011). Dust- and mineral-iron utilization by the marine dinitrogen-fixer *Trichodesmium*. *Nature Geoscience*, *4*(8), 529–534. https://doi.org/10.1038/ngeo1181

Rueter, J. G., McCarthy, J. J., & Carpenter, E. J. (1979). The toxic effect of copper on *Oscillatoria* (*Trichodesmium*) *thiebautii*. *Limnology & Oceanography*, *24*(3), 558–562. https://doi.org/10.4319/lo.1979.24.3.0558

Schladitz, A., Müller, T., Kaaden, N., Massling, A., Kandler, K., Ebert, M., et al. (2009). *In situ* measurements of optical properties at Tinfou (Morocco) during the saharan mineral dust experiment SAMUM 2006. *Tellus Series B Chemical and Physical Meteorology*, *61*(1), 64–78. https://doi.org/10.1111/j.1600-0889.2008.00397.x

Shaked, Y. (2008). Iron redox dynamics in the surface waters of the Gulf of Aqaba, Red Sea. *Geochimica et Cosmochimica Acta*, *72*(6), 1540–1554. https://doi.org/10.1016/j.gca.2008.01.005

Shaked, Y., de Beer, D., Wang, S., Zhang, F., Visser, A. N., Eichner, M., & Basu, S. (2023). Co-acquisition of mineral-bound iron and phosphorus by natural *Trichodesmium* colonies. *Limnology & Oceanography*, 1–14. https://doi.org/10.1002/lno.12329

Shaked, Y., & Lis, H. (2012). Disassembling iron availability to phytoplankton. *Frontiers in Microbiology*, *3*(APR), 1–26. https://doi.org/10.3389/fmicb.2012.00123

Stockdale, A., Krom, M. D., Mortimer, R. J. G., Benning, L. G., Carslaw, K. S., Herbert, R. J., et al. (2016). Understanding the nature of atmospheric acid processing of mineral dusts in supplying bioavailable phosphorus to the oceans. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(51), 14639–14644. https://doi.org/10.1073/pnas.1608136113

Taboada, F. G., Gil, G. R., Höfer, J., González, S., & Anadón, R. (2010). *Trichodesmium* spp. population structure in the eastern North Atlantic subtropical gyre. *Deep-Sea Research Part I Oceanographic Research Papers*, *57*(1), 65–77. https://doi.org/10.1016/j.dsr.2009.09.005

Tang, W., Cerdán-García, E., Berthelot, H., Polyviou, D., Wang, S., Baylay, A., et al. (2020). New insights into the distributions of nitrogen fixation and diazotrophs revealed by high-resolution sensing and sampling methods. *ISME Journal*, *14*(10), 2514–2526. https://doi.org/10.1038/s41396-020-0703-6

Tyrrell, T., Marañón, E., Poulton, A. J., Bowie, A. R., Harbour, D. S., & Woodward, E. M. S. (2003). Large-scale latitudinal distribution of *Trichodesmium* spp. in the Atlantic Ocean. *Journal of Plankton Research*, *25*(4), 405–416. https://doi.org/10.1093/plankt/25.4.405

Villareal, T. A., & Carpenter, E. J. (1990). Diel buoyancy regulation in the marine diazotrophic cyanobacterium *Trichodesmium thiebautii*. *Limnology & Oceanography*, *35*(8), 1832–1837. https://doi.org/10.4319/lo.1990.35.8.1832

Villareal, T. A., & Carpenter, E. J. (2003). Buoyancy regulation and the potential for vertical migration in the oceanic cyanobacterium *Trichodesmium*. *Microbial Ecology*, *45*(1), 1–10. https://doi.org/10.1007/s00248-002-1012-5

Walsby, A. E. (1978). The properties and buoyancy-providing role of gas vacuoles in *Trichodesmium* Ehrenberg. *British Phycological Journal*, *13*(2), 103–116. https://doi.org/10.1080/00071617800650121

Walsby, A. E. (1992). The gas vesicles and buoyancy of *Trichodesmium*. In J. G. Carpenter, E. J. Capone, D. G. Rueter (Ed.), *Marine pelagic cyanobacteria: Trichodesmium and other diazotrophs* (pp. 141–161). Springer. https://doi.org/10.1007/978-94-015-7977-3_9

Wang, S., Koedooder, C., Zhang, F., Kessler, N., Eichner, M., Shi, D., & Shaked, Y. (2022). Colonies of the marine cyanobacterium *Trichodesmium* optimize dust utilization by selective collection and retention of nutrient-rich particles. *iScience*, *25*(1), 103587. https://doi.org/10.1016/j.isci.2021.103587

Wang, S., Zhang, F., Koedooder, C., Qafoku, O., Basu, S., Krisch, S., et al. (2023). Calculations and simulations of dust factor (K) and sinking velocity of particle-free *Trichodesmium* colonies (v0) [Software]. *Zenodo*. https://doi.org/10.5281/zenodo.10290901

White, A. E., Spitz, Y. H., & Letelier, R. M. (2006). Modeling carbohydrate ballasting by *Trichodesmium* spp. *Marine Ecology Progress Series*, *323*(Oliver 1994), 35–45. https://doi.org/10.3354/meps323035

Yang, T., Chen, Y., Zhou, S., & Li, H. (2019). Impact of copper on marine phytoplankton: A review. *Atmosphere*, *10*(414), 599–602. Retrieved from http://inis.iaea.org/search/search.aspx?orig_q=RN:41131251

Zehr, J. P., & Capone, D. G. (2020). Changing perspectives in marine nitrogen fixation. *Science*, *368*(6492). https://doi.org/10.1126/science.aay9514

Zhang, C., Ito, A., Shi, Z., Aita, M. N., Yao, X., Chu, Q., et al. (2019). Fertilization of the Northwest Pacific ocean by East Asia air pollutants. *Global Biogeochemical Cycles*, *33*(6), 690–702. https://doi.org/10.1029/2018GB006146

References From the Supporting Information

Ho, T.-Y. (2012). Nickel limitation of nitrogen fixation in Trichodesmium. *Limnology and Oceanography*, *58*(1), 112–120. https://doi.org/10.4319/lo.2013.58.1.0112

Sunda, W. G., & Huntsman, S. A. (1998). Processes regulating cellular metal accumulation and physiological effects: Phytoplankton as model systems. *Science of The Total Environment*, *219*(2–3), 165–181. https://doi.org/10.1016/s0048-9697(98)00226-5

Tiesinga, E., Mohr, P. J., Newell, D. B., & Taylor, B. N. (2021). CODATA recommended values of the fundamental physical constants: 2018. *Reviews of Modern Physics*, *93*(2). https://doi.org/10.1103/revmodphys.93.025010

Walsby, A. E., & McAllister, G. K. (1987). Buoyancy regulation by microcystisin Lake Okaro. *New Zealand Journal of Marine and Freshwater Research*, *21*(3), 521–524. https://doi.org/10.1080/00288330.1987.9516249