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Theoretical constraints on *Trichodesmium* colony size: The role of carbon dioxide and light

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ABSTRACT

Size is an important trait among marine phytoplankton as it influences a vast range of physiological, ecological, and evolutionary processes. For *Trichodesmium*, a cyanobacterial diazotroph important for the global nitrogen cycle, size is a flexible trait that can change because of its ability to form colonies. *Trichodesmium* colonies can persist from 10 μm to greater than 1 mm in the natural environment. Despite this known ability, we still do not know whether a maximum size limit exists for *Trichodesmium* colonies and, more importantly, whether any mechanisms regulate this limit. In this paper, we use a theoretical metabolic model to investigate the role of two factors known to influence *Trichodesmium* colony size: carbon dioxide and light availability. The greater the availability of carbon dioxide or the average light availability, the greater the potential colony size of *Trichodesmium*. Carbon limitations have a much stronger effect on colony sizes than light limitations. Higher respiratory costs, perhaps due to higher water temperatures, do not appear to limit maximum colony sizes unless they consume nearly all the carbon that is fixed. Our theoretical model highlights several scenarios that likely assert some control over the ecology of *Trichodesmium* in the global ocean. It also implies that natural colonies must have mechanisms to escape from carbon limitations. To achieve sizes like 1 mm, *Trichodesmium* colonies must be highly porous (>91%) or live in environments with a nutrient flux 12 times greater than what molecular diffusion can provide.

1. Introduction

Trichodesmium is a marine cyanobacterium with a widespread global distribution (Delmont 2021). In the natural environment, *Trichodesmium* can exist as individual cells, small trichomes, and large colonies (González Taboada et al. 2010; Pierella Karlusich et al. 2021). Given its significant role in the global nitrogen cycle (Capone et al. 1997), understanding the morphotype and reasons for colony formation is crucial for determining nitrogen inputs into the ocean. For example, experimental evidence has shown that *Trichodesmium* trichomes and colonies have different carbon and nitrogen fixation rates (Eichner et al. 2019). This implies that major changes in *Trichodesmium* colony formation rates can have knock-on effects on other components of the marine microbial food web.

Colony formation in *Trichodesmium* largely occurs through the process of aggregation: where individual filaments come together, especially under stressful conditions, to form larger puffs, tufts, or irregular shapes (Eichner et al. 2023). These aggregates (i.e., colonies) have the powerful ability to modulate their shape based on environmental conditions and the gliding behavior of individual filaments (Pfreundt et al. 2023). Recent work has explored the complex reasons for colony formation in *Trichodesmium*, including, but not limited to, the role of respiration (Agarwal et al. 2022), buoyancy effects (Held et al. 2022), enhanced nutrient uptake (Tzubari et al. 2018), mutualistic interactions with epibionts (Frischkorn et al. 2017, 2018), etc. Despite this range of reasons, it is still unclear whether *Trichodesmium* has a maximum colony size. Size in marine phytoplankton is considered a master trait, often correlated to other vital rates (Litchman and Klausmeier 2008; Marañón 2015). Given the complexity surrounding *Trichodesmium* colony formation, determining maximum colony sizes might allow for better parameterization of earth system models that typically incorporate *Trichodesmium* as a key component.

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For earth system models aiming to project future *Trichodesmium* abundance and distribution, it is essential to consider the impact of environmental factors, especially in relation to enhanced carbon dioxide (CO_2) and light availability, both of which are known to influence *Trichodesmium*'s metabolism (Kranz et al. 2010; Levitan et al. 2010; Garcia et al. 2011; Boatman et al., 2017, 2018; Yi and Gao 2023). In brief, high carbon dioxide concentrations increase nitrogen fixation rates, but this effect is highly modulated by light levels (Kranz et al. 2010; Garcia et al. 2011; Yi and Gao 2023). The highest growth rates are typically observed under high pCO_2 and high light conditions (Kranz et al. 2010; Boatman et al., 2017, 2018), which may be attributed to key changes in protein activity and a reduced investment in protein biosynthesis (Levitan et al. 2010). *Trichodesmium* trichome length is greatest under low and medium light, whereas increased CO_2 has no reported effect on trichome length (Garcia et al. 2011; Yi and Gao 2023). Although the overall effects of increased CO_2 on *Trichodesmium* growth are complex and context-dependent, influenced by interactions with other environmental factors such as temperature and pH, there is even less understanding of how CO_2 or light levels may affect overall colony size or morphology.

Within this context, we aim to answer the following questions: (i) Is there a maximum colony size for *Trichodesmium*? and (ii) What are the limiting factors that determine *Trichodesmium* colony size? To address these questions, we develop a model that assumes a large spherical colony of cells that is permitted to grow or decrease in size. Model colonies are assumed to be immersed in a homogenous, well-mixed environment with stable background concentrations of dissolved gases such as oxygen and carbon dioxide. The diffusion rates of these gases into the colony, alongside light availability and carbon fixation rates, are varied to understand the potential effects on maximum colony size. A detailed description of the model equations can be found in Section 3.

2. Results and Discussion

2.1. Carbon limitations

Although dissolved inorganic carbon in the ocean can exist in three forms (CO_2, HCO_3^- and CO_3^{2-}), marine phytoplankton typically rely on dissolved CO_2 for growth and can be limited by its availability at the cell surface (Riebesell et al. 1993). To circumvent such limitations, cells tend to have multiple strategies for enhancing carbon dioxide uptake. Most phytoplankton, for example, have specific carbon-concentrating mechanisms (Reinfelder 2011) that enhance internal carbon dioxide concentrations. Many of these mechanisms are driven by carbonic anhydrases (CA), which are found in diverse forms across marine phytoplankton taxa (Jensen et al. 2020). In cyanobacteria, carbon-concentrating mechanisms are considered highly effective and capable of concentrating CO_2 by many times around the active site of Rubisco (Badger and Price 2003). Despite these strategies, there are additional considerations for marine phytoplankton that rely on carbon acquisition. One such consideration is the role of cell size in determining the diffusive uptake of carbon dioxide from the environment. As cells (or colonies) get larger, their surface area increases more slowly than their total cell volume. In theory, this suggests that there is a limit to size where diffusive uptake can no longer support the carbon fixation requirement of the colony to maintain biomass (Beardall et al. 2009). Alternatively, recent evidence suggests that larger cells may also have a greater ability to upregulate carbon-concentrating mechanisms, which can allow them to achieve greater growth rates and maximum biovolume densities (Malerba et al. 2021). *Trichodesmium*, a marine cyanobacterium that can exist across a range of cell sizes, has also been shown to be CO_2-limited in large colonies (Tchernov and Lipschultz 2008).

In this paper, we investigate whether carbon limitations might determine the maximum colony sizes for *Trichodesmium*. The supply of CO_2 was modeled by increasing or decreasing γ, the CO_2-diffusion rate, independent of the mechanism involved. The diffusion coefficient of CO_2 in seawater is approximately $2 \times 10^{-9}\ m^2s^{-1}$ ($2000\ \mu m^2s^{-1}$; null case). We assumed a reduction in this rate due to cell membrane layers and set the diffusion rate to $4\ \mu m^2s^{-1}$ (MaCDougall and McCabe 1967), based on experiments conducted on bacteria. We did not estimate further reductions in the diffusion rate within the colony as studies have only shown a marginal reduction in gas diffusivity in marine aggregates (Ploug et al. 2008). Instead, we tested greater gas diffusivity rates (4, 2000, and 24,000 μm^2s^{-1}) to estimate the potential influence of CO_2 on *Trichodesmium* colony size.

Fig. 1 highlights the potential growth of model colonies over a period of 5 years under different values of γ. In the low-diffusion case, where CO_2 diffusion rates were set to $4\ \mu m^2 s^{-1}$, *Trichodesmium* colonies could not sustain themselves and slowly reduced in size. Interestingly, setting the diffusion rate to $2000\ \mu m^2s^{-1}$ (i.e., no restrictions due to cell membrane layers) increased the maximum limit to $304\ \mu m$. In the extreme scenario where γ was set to 24,000 μm^2s^{-1}, colonies reached $1.05 \times 10^3\ \mu m$ in 5 years. If all else were equal, these results suggest that carbon limitations would naturally limit colony sizes, and an increase in the carbon availability, whether passively or due to an active process, would allow *Trichodesmium* colonies to support greater biomass. On average, real *Trichodesmium* colonies have around $\sim$ 30,000 cells per colony (LaRoche and Breitbarth 2005), which would approximate a model colony size of $\sim$ 320 μm. Likely, as real colonies are not packed spheres and naturally allow for greater carbon diffusion due to irregular morphology, realistic colonies would be less carbon-limited than our model colonies. We tested a wide range of carbon diffusion rates, including 24,000 μm^2s^{-1}, to account for these potential differences in theoretical and actual colony morphology. In the lab, *Trichodesmium* colonies have been observed to form after the exponential growth phase (Chen et al. 1996; Bell et al. 2005). For our model, diffusion rates 12 times greater than passive diffusion allowed colonies to reach that size in about 2 years under constant light. Although 1 mm is conventionally considered the maximum size of *Trichodesmium* colonies in nature, to our knowledge, no systematic studies have verified this limit.

These results point to two important conclusions. First, even though we model colonies as solid spheres, *Trichodesmium* colonies are loose aggregates of individual trichomes. In simulations where the porosity of colonies was increased to 91% (Fig. S1), *Trichodesmium* colonies could

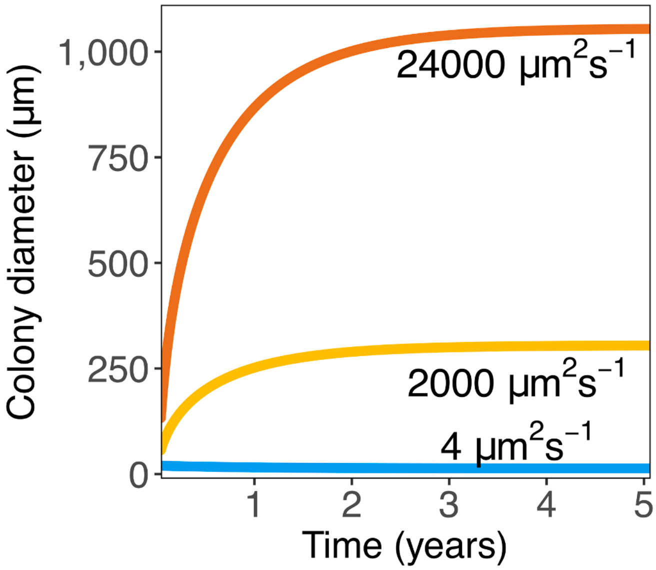

Fig. 1. Carbon dioxide diffusion rates (γ) determine the maximum size a colony can achieve. $\gamma = 4\ \mu m^2s^{-1}$ (blue), $2000\ \mu m^2s^{-1}$ (yellow), and $24000\ \mu m^2s^{-1}$ (red). The average light intensity was set to 700 $\mu mol\ photons\ m^{-2}s^{-1}$.

achieve 1 mm sizes with $\gamma = 2000\ \mu m^2 s^{-1}$. Second, real colonies likely do not need years to reach 1 mm. The difference is in the method of colony formation, as real colonies can rely on aggregation and not just colony-specific growth. Theoretically, the attachment of multiple filaments would form a colony fairly quickly; however, the maximum colony size would still be subject to the same diffusive constraints.

2.2. Light limitations

As photoautotrophs, natural *Trichodesmium* populations are sensitive to ambient light conditions. In general, experiments that expose *Trichodesmium* to different levels of light show an increase in growth rates under high light (Bell and Fu 2005; Ho et al. 2013; Boatman et al. 2018; Lu et al. 2018). Such a response is made possible with photoprotective mechanisms and the role of superoxide dismutases, which can reduce oxidative stress under high solar radiation (Ho et al. 2013; Chen et al. 2022). Like many cyanobacteria, *Trichodesmium* is also sensitive to the spectral quality of available light (Rodriguez and Ho 2017; Zhu et al. 2022), which may be relevant for models of phytoplankton community structure that resolve chromatic adaptation (Hickman et al. 2010). Recent evidence also suggests that *Trichodesmium* can fix nitrogen in the absence of light, potentially using photosynthetically-derived carbon (Benavides et al. 2022). When taken together, the role of light and its relative availability may have significant effects on the rates of carbon and nitrogen fixation for *Trichodesmium* in a changing ocean.

Despite the importance of light to the *Trichodesmium* metabolism, the role of light limitations in *Trichodesmium* colony formation is less understood. Some evidence suggests colony formation, in conjunction with daytime nitrogen fixation, may be used to enhance light availability for *Trichodesmium* by increasing its buoyancy (Held et al. 2022). Self-shading within colonies may also reduce the specific absorption per unit of pigment and play a photoprotective role under high light conditions (Lewis et al. 1988). Conversely, this also implies that under low-light conditions, it may be disadvantageous to exist as larger colonies (Prufert-Bebout et al. 1993).

When we subjected our model colonies to three different levels of constant light—70, 200, and 700 $\mu mol\ photons\ m^{-2} s^{-1}$, they performed well at every light level (Fig. 2). This is in agreement with experiments where growth has been observed at light levels as low as 10 $\mu mol\ photons\ m^{-2} s^{-1}$ (Bell and Fu 2005). The maximum colony size was different under different light levels, reaching the greatest size with 700 $\mu mol\ photons\ m^{-2} s^{-1}$.

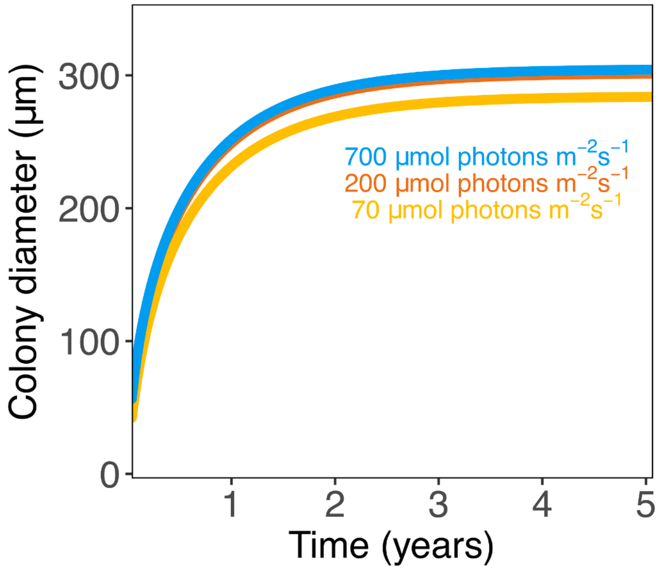

Fig. 2. Light availability (I) alters maximum colony size. Low light ($I = 70\ \mu mol\ photons\ m^{-2} s^{-1}$; yellow), medium light ($I = 200\ \mu mol\ photons\ m^{-2} s^{-1}$; red), and high light ($I = 700\ \mu mol\ photons\ m^{-2} s^{-1}$; blue). Each line indicates the colony size (diameter; µm) over a period of 5 years. The carbon dioxide diffusion rate (γ) was set to $2000\ \mu m^2 s^{-1}$.

A critical parameter that determines our model colonies' response to available light levels is λ, the light saturation coefficient. The light saturation coefficient determines the light level at which growth may be saturated. When λ is doubled, the required light to achieve the same response is halved. Although we set λ to 0.01 based on previous studies with similar models (Inomura et al. 2019; Gao et al. 2024), experimental evidence has reported *Trichodesmium* to be light saturated at 100 – 300 $\mu mol\ photons\ m^{-2} s^{-1}$ (Carpenter and Roenneberg 1995; Breitbarth et al. 2008; Cai et al. 2015). By fixing λ to 0.01 $\mu mol\ photons^{-1}\ m^2 s^1$, we were able to focus on varying a single parameter to test for light limitations. Increasing λ would reduce the light requirements for *Trichodesmium* colonies and alter their growth rate, but it would only have a marginal effect on maximum colony size (Fig. S2). Colonies could acquire a greater light saturation coefficient to survive in low light or an increased maximum photosynthesis rate, which can be achieved by allocating more photosynthetic molecules (Inomura et al. 2020).

The results for both carbon and light limitation model experiments suggest that *Trichodesmium* is more sensitive to carbon depletion than to self-shading (or decreased light levels). This implies that processes that affect carbon availability (e.g., ocean CO_2 uptake) will have a larger effect on *Trichodesmium* colony sizes in the natural environment, as opposed to processes that alter light availability (e.g., changes in stratification or upwelling). Future studies may need to include additional parameters, such as temperature and pH levels, to accurately project trends in *Trichodesmium* colony size on a global scale.

2.3. Relative respiration rates and colony growth

Determining metabolic limitations requires an understanding of not only processes that determine growth, such as carbon fixation, but also the role of cell maintenance and respiratory costs. In a previous study, the role of cell respiration was influential in determining the success of colonies *vs* individual trichomes (Agarwal et al. 2022). In theory, higher respiratory costs, often associated with cell stress, would allow colonies to persist longer than individual trichomes, even with lower overall carbon and nitrogen fixation rates.

Respiratory costs (F_{res}) were initially set to determine a maximum colony size for *Trichodesmium* under ideal conditions (Fig. 3; yellow line). This constant respiration rate was 40% of the initial carbon fixation rate (F_{cfix}). By the end of the simulation, it increased to 94.82736% of F_{cfix}, largely because carbon limitations drove F_{cfix} down. As real colonies can modulate their growth and maintenance processes, allowing respiratory costs to vary as a proportion of carbon fixation can provide additional insight into the overall constraints of the *Trichodesmium* metabolism as it relates to colony sizes.

When respiration was fixed to a proportion of the carbon fixation rate, colony growth was still observed, albeit at different rates. Respiratory costs that consume 92% of the carbon fixed per hour allowed the model colonies to reach greater than 400 µm in 5 years (Fig. 3; red line) with continued rapid increases. The difference in the colony growth function implies that 92% of the carbon fixed is too low a cost. On the other hand, model colonies slowly reduced in size when respiratory costs were set to 95% of the carbon fixation rate (Fig. 3; blue line), implying that 95% is too high a cost for growth. Our results suggest that carbon loss processes would be unlikely to limit *Trichodesmium* colony size over long periods of time, unless they are nearly consuming all the carbon that is fixed. Overall, it seems improbable that higher respiratory costs, perhaps due to higher water temperature (Barton et al. 2020), would have any discernible effect on *Trichodesmium* maximum colony size.

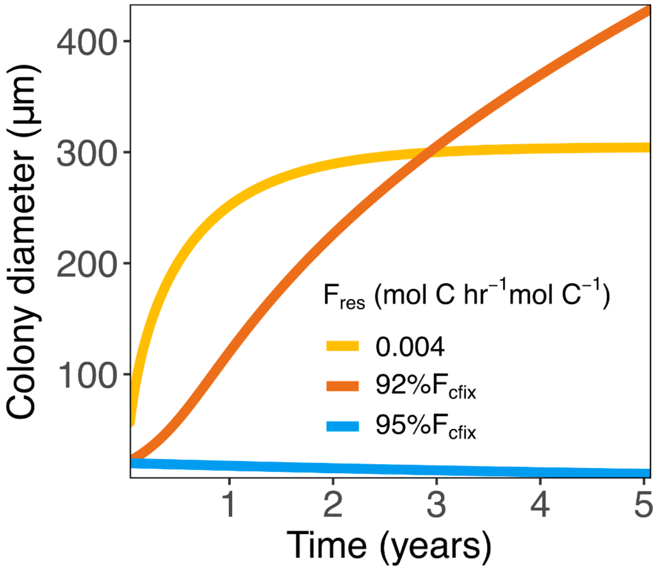

Fig. 3. Respiration rates (F_{res}) can change the limit and pace of colony growth. $F_{res} = 0.004$ mol C hr^{-1} mol C (yellow), $F_{res} = 92\% F_{cfix}$ (red), and $F_{res} = 95\%$ F_{cfix} (blue). Each line indicates the colony size (radius; μm) over 5 years. Note: The blue line indicates a slow decrease in colony size.

2.4. *Study limitations and future directions*

Although it is generally expected that colonies experience greater light and carbon limitations than single trichomes (Eichner et al. 2023), it was unclear *how much* of an effect these factors can have on maximum colony size. We found that *Trichodesmium* does get limited by carbon dioxide diffusion and light availability, and that these limitations can mostly explain observed colony sizes. However, other potential constraints were not included in the model and warrant further discussion.

2.4.1. *H1: Iron or other micronutrient limitations*

Trichodesmium colony formation has been experimentally linked to the acquisition of nutrients such as iron and phosphorus from dust particles (Basu and Shaked 2018; Kessler et al. 2020; Wang et al. 2022). As our model assumes a nutrient-replete environment, colony size limitations may be driven by the natural availability of iron, which would limit nitrogen fixation (Berman-Frank et al. 2001). One possible method to test this hypothesis would be to measure the size of *Trichodesmium* colonies in nutrient-rich culture media over a long-period of time.

2.4.2. *H2: Ecological constraints, such as microzooplankton grazing and viral lysis*

While laboratory experiments can typically allow for the control of microenvironment influence, the role of ecological influence can often be challenging to estimate in the lab. Several studies have reported *Trichodesmium* as an important food source for grazers (O'Neil 1998; Conroy et al. 2017; Mos et al. 2024). Meanwhile, the activity of viruses has also been suggested as a potential control on *Trichodesmium* populations (Hewson et al. 2004; Brown et al. 2013). Under this scenario, observed colony sizes of *Trichodesmium* may be limited by variations in grazer predation or the likelihood of viral infection, which may preferentially target the largest colonies.

2.4.3. *H3: Turbulent flows*

The natural environment exposes *Trichodesmium* to turbulence, which may physically break apart the largest colonies and limit maximum colony size (Naselli-Flores et al. 2021). One recent study has also demonstrated how the ambient flow field may alter *Trichodesmium* colony growth rates and determine their overall morphology (Wei et al. 2023). Since molecular diffusion is insufficient to explain colony sizes > 304 μm, turbulence could also explain how additional nutrients are delivered to carbon-limited colonies.

2.4.4. *H4: Genetic triggers or other cues*

Trichodesmium, like many other colonial phytoplankton, can often be described as exhibiting "social" behavior by forming aggregates (e.g., Eichner et al. 2023). This description is based on the assumption that colonies' behavior may represent societies with many individual components. With such an assumption, colony growth is inhibited by external factors, such as carbon dioxide or light limitation.

An additional possibility is that *Trichodesmium* colony size may be limited by internal constraints, perhaps similar to how size in insects, dogs, and humans is regulated by hormonal networks (Bernstein 2010), and is subject to ecological and evolutionary developmental constraints (Burness et al. 2001; Okie et al. 2013; Galis et al. 2018). A broader implication of this hypothesis is that *Trichodesmium* colony formation may be viewed as a form of multicellularity alongside a demonstration of sociality.

3. Materials and Methods

We assume that a spherical colony of *Trichodesmium* with radius r consists of ℵ cells, each with volume V^{cell}. Colonies that have a larger radius either have (i) larger cells (greater cell volume) or, (ii) more cells (greater ℵ). For this analysis, we keep V^{cell} fixed at 575 μm^3 per cell. To account for porosity, V^{cell} can be divided by $(1 - p)$, where p is the

Table 1
List of model parameters, their descriptions, and units. * indicates that the variable can be time-varying.

Variable	Description	Units	Initial/ Constant Value
ℵ	Number of cells in a colony	cell	7*
r	Radius of a spherical colony	μm	10*
$\mathbf{V^{cell}}$	Volume per cell	μm^3 cell^{-1}	575
$\mathbf{C_{sto}}$	Total carbon storage in a colony (biomass)	mol C	3.28 x 10^{-10}*
$\mathbf{Y^{C:cell}}$	Ratio describing how much carbon is contained in a cell	mol C cell^{-1}	4.5 x 10^{-11}
$\mathbf{F_{cfix}}$	Carbon fixation rate	mol C h^{-1} mol C^{-1}	0.010*
$\mathbf{F_{nfix}}$	Nitrogen fixation rate	mol N h^{-1} mol N^{-1}	0.004*
$\mathbf{Y^{C:N}}$	Carbon-to-nitrogen conversion for nitrogen fixation	mol C mol N^{-1}	1
$\mathbf{R_{N:C}}$	Cellular nitrogen to carbon ratio	mol N mol C^{-1}	0.129
$\mathbf{F_{res}}$	Respiration rate	mol C h^{-1} mol C^{-1}	0.004*
$\mathbf{F_{maxC}}$	Maximum possible carbon fixation rate	mol C h^{-1} mol C^{-1}	0.1
λ	Light saturation coefficient	μmol photons^{-1} m^{2}s	0.01
I	Average light intensity for the colony	μmol photons m^{-2}s^{-1}	700*
$[\mathbf{intCO_2}]$	Internal carbon dioxide concentration	mol CO$_2$ m^{-3}	0.0205*
$[\mathbf{extCO_2}]$	External carbon dioxide concentration	mol CO$_2$ m^{-3}	0.0205
$\mathbf{K_c}$	Half-saturation constant for C	mol CO$_2$ m^{-3}	0.05
β	Oxygen diffusivity coefficient	μm^{2}s^{-1}	2000
γ	Carbon dioxide diffusivity coefficient	μm^{2}s^{-1}	2000
$[\mathbf{extO_2}]$	External oxygen concentration	mol O$_2$ m^{-3}	0.25625
$[\mathbf{intO_2}]$	Internal oxygen concentration	mol O$_2$ m^{-3}	0.25625*
$\mathbf{Y^{O_2:CO_2}}$	Ratio describing how much oxygen is created when carbon is fixed	mol O$_2$ mol CO$_2^{-1}$	1
$\boldsymbol{\tau}$	Ratio of carbon fixation rate to nitrogen fixation rate	–	2.5

porosity value (e.g., 0.95).

$$\aleph = \frac{4}{3} \times \frac{\pi r^3}{V^{cell}} \tag{1}$$

The total amount of biomass in a colony (C_{sto}) in mol C varies through time based on the processes of carbon fixation, nitrogen fixation, and respiration occurring in each colony cell. Each process is scaled by the number of cells present in the colony ($\aleph$) and the carbon content of each cell ($Y^{C:cell}$). F_{cfix} and F_{nfix} refer to the carbon fixation and nitrogen fixation rates. $Y^{C:N}$ is the carbon-to-nitrogen conversion for nitrogen fixation, $R_{N:C}$ is the cellular nitrogen to carbon ratio and F_{res} is the respiration rate. We assume a constant F_{res} of the colony, representing carbon losses due to cell maintenance and repair. There are no external nitrogen sources in this model. Refer to Table 1 for the units and initial values of these parameters.

$$\begin{aligned}\frac{d[intO_2]}{dt} &= \frac{4\pi r\beta([extO_2] - [intO_2]\,) \times 3600}{\frac{4}{3}\pi r^3} + \frac{Y^{C:cell}}{V^{cell} \times 10^{-18}} F_{cfix} Y^{O_2:CO_2} - \frac{Y^{C:cell}}{V^{cell} \times 10^{-18}} F_{res} Y^{O_2:CO_2} \\ &= \frac{10800\beta([extO_2] - [intO_2]\,)}{r^2} + \frac{Y^{C:cell}}{V^{cell} \times 10^{-18}} F_{cfix} Y^{O_2:CO_2} - \frac{Y^{C:cell}}{V^{cell} \times 10^{-18}} F_{res} Y^{O_2:CO_2}\end{aligned} \tag{5}$$

$$\begin{aligned}\frac{d[intCO_2]}{dt} &= \frac{4\pi r\gamma([extCO_2] - [intCO_2]) \times 3600}{\frac{4}{3}\pi r^3} - \frac{Y^{C:cell}}{V^{cell} \times 10^{-18}} F_{cfix} + \frac{Y^{C:cell}}{V^{cell} \times 10^{-18}} F_{res} \\ &= \frac{10800\gamma([extCO_2] - [intCO_2])}{r^2} - \frac{Y^{C:cell}}{V^{cell} \times 10^{-18}} F_{cfix} + \frac{Y^{C:cell}}{V^{cell} \times 10^{-18}} F_{res}\end{aligned} \tag{6}$$

$$\frac{dC_{sto}}{dt} = \aleph Y^{C:cell}(F_{cfix} - F_{nfix} Y^{C:N} R_{N:C} - F_{res}) \tag{2}$$

Consequently, colony growth or decay is represented by a change in the number of cells. When $\frac{dC_{sto}}{dt}$ is negative, the colony loses cells, and when $\frac{dC_{sto}}{dt}$ is positive, the colony gains cells. $\frac{dC_{sto}}{dt}$ is divided by $Y^{C:cell}$ to calculate the change in the number of cells.

The rate of carbon fixation for each colony depends on the average light availability (I), the light saturation coefficient (λ), and the carbon dioxide concentration available within the colony ($[intCO_2]$). Carbon fixation saturates at high light and has a maximum possible rate (F^{maxC}). We represent carbon dioxide as a substrate and model its dependence using Monod kinetics with a half-saturation constant K_c (Young et al. 2016).

$$F_{cfix} = F^{maxC}\left(1 - e^{-\lambda I}\right)\left(\frac{[intCO_2]}{K_c + [intCO_2]}\right) \tag{3}$$

Similarly, nitrogen fixation for each colony cell is assumed to vary linearly with carbon fixation rates. τ represents the ratio of F_{cfix} to F_{nfix}.

$$F_{nfix} = \frac{F_{cfix}}{\tau} \tag{4}$$

The gaseous fluxes for the colony depend on diffusion from the external environment and the metabolic processes. The diffusivity coefficient across cell membranes for both oxygen (β) and carbon dioxide (γ) was assumed to be constant (MacDougall and McCabe 1967). $[extO_2]$ and $[extCO_2]$ refer to the external concentrations of O_2 and CO_2. $Y^{O_2:CO_2}$ is the ratio describing how much oxygen is created when carbon dioxide is fixed. Both equations 5 and 6 tie back into equation 3, where carbon fixation rates are calculated at every time step. The term $4\pi r$ models the diffusion of gas towards the center of a sphere under steady-state conditions (Armstrong 2008), and the factor 3600 is for the conversion of second-scale fluxes into hourly-scale units. The factor 10^{-18} is for the conversion of μm^3 to m^3. $\frac{Y^{C:cell}}{V^{cell} \times 10^{-18}}$ is the term for biomass density ($mol\,C\,m^{-3}$).

We assume that each cell within the colony can allocate resources effectively and rapidly. Any effects of diffusive limitations are thus shared across the entire colony and not localized to any specific section (e.g., the center of the colony). Likely, the morphology of natural colonies increases growth efficiency and confers fitness advantages because of resource sharing (Kempes et al. 2014). Thus, $[intO_2]$ and $[intCO_2]$ refer to the average gas concentration within each cell of the entire colony.

The model was run using the R package ‘deSolve’ with the ‘lsoda’ method and a step-size of 0.01 (Soetaert et al. 2010) at an hourly scale for a total time of 5 years. In all cases, the model output for the first 2 weeks was removed to allow for model stabilization and a floor of 10^{-12} was implemented to prevent zeros or negatives (across internal gas concentrations, total biomass, and colony size). For each model run, we assumed stable background concentrations of oxygen and carbon dioxide ($[extO_2]$ and $[extCO_2]$). Halving $[extCO_2]$ reduced the maximum colony size to 66% of the original, and doubling $[extCO_2]$ increased it to 146% of the original (Fig. S3).

3.1. Software

Model construction, analysis, and figure preparation were done in R (R Core Team 2024). We used the R packages ‘deSolve’, ‘tidyverse’, and ‘cowplot’ (Soetaert et al. 2010; Wickham et al. 2019; Wilke 2020).

3.2. Author contributions

VA conducted the analysis and wrote the first draft of the manuscript. VA, KI, and SC developed the concept of the study and the numerical model. VA, KI, SC, AC, and CBM assisted in the development of figures and the preparation of the final manuscript.

3.3. Data Availability

Code is available on Zenodo (https://doi.org/10.5281/zenodo.19175311).

CRediT authorship contribution statement

Vitul Agarwal: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Keisuke Inomura:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Subhendu Chakraborty:** Writing – review & editing, Visualization, Validation, Supervision, Methodology, Investigation, Conceptualization. **Audrey Ciochetto:** Writing – review & editing, Visualization, Validation, Resources, Project administration, Methodology, Investigation. **Colleen B. Mouw:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jtbi.2026.112446.

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