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A physiological model for the marine cyanobacteria, *Trichodesmium*

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Abstract: Nitrogen fixation by the marine cyanobacterium, *Trichodesmium,* is believed to form a substantial component of the nitrogen budget of the Great Barrier Reef Lagoon. Here, we present a new, physiologically-based model to predict the distribution and growth of *Trichodesmium.* The model has been incorporated into a large-scale, process-based, three-dimensional hydrodynamic, sediment dynamic and biogeochemical model of the Great Barrier Reef Lagoon through eReefs, a major collaborative project that is developing near-real-time and forecasting models to inform management of this important environmental asset.

The model simulates the growth and respiration of *Trichodesmium* colonies, along with uptake of nutrients, fixation of atmospheric nitrogen, changes in cellular buoyancy, grazing by zooplankton and death associated with lysis by cyanophages. To facilitate improved simulation of nutrient dynamics as well as changes in carbohydrate ballasting (which affects buoyancy), the model allows variable intracellular C:N:P:Chlorophyll *a* ratios. Chlorophyll *a* accumulation and *Trichodesmium* growth depend on the intracellular availability of nutrients and fixed carbon. Carbon accumulation is a function of the spectrally resolved light environment, so that changes in light quality as well as light intensity may affect growth. As *Trichodesmium* colonies accumulate carbon, their buoyancy decreases, allowing the vertical movement of *Trichodesmium* through the water column to be simulated.

Particular attention is paid to simulating the nitrogen dynamics of *Trichodesmium*. Where sufficient ammonium is available in the water column, this is taken up preferentially, reflecting the lower energetic cost of this nitrogen source. When external ammonium concentrations are not sufficient to supply the cellular demand, *Trichodesmium* colonies take up nitrate. A novel model formulation is presented to simulate this preferential uptake dynamic without introducing an additional parameter. Only if the supply of dissolved inorganic nitrogen is insufficient do nitrogen fixation pathways become active in *Trichodesmium* cells. In this case, the growth rate of *Trichodesmium* is reduced in proportion to the energetic cost (in terms of ATP) of nitrogenase activity. With few exceptions, the values of parameters used in the model can be derived from direct measurements or theory.

Important processes not included in the model are also discussed; these include iron limitation of nitrogen fixation and the dynamics of surface scum. Unfortunately, it is not possible at this stage to include iron limitation, as iron inputs to the Great Barrier Reef Lagoon are not monitored; hence, iron is not included in the biogeochemical model. The dynamics of surface accumulations of buoyant *Trichodesmium* are an interesting problem in terms of physics, chemistry and biological processes, and may be considered in a future version of the model.

Keywords: *Physiological model, nitrogen fixation, eReefs*

1. INTRODUCTION

eReefs is a large, collaborative project that is building catchment and marine models for Australia's Great Barrier Reef Lagoon (GBRL), a world-heritage environmental asset. The eReefs package includes three-dimensional mechanistic biogeochemical, sediment and hydrodynamic models for the entire GBRL, implemented in Environmental Modelling Suite (EMS) (Margvelashvili et al. 2013; Wild-Allen 2013) and nested within global hydrodynamic models, along with catchment models to predict sediment and nutrient loads to the GBRL (Robson and Dourdet 2013; Dourdet and Robson submitted).

Nitrogen fixation by *Trichodesmium* is believed to form a substantial component of the nitrogen budget of the Great Barrier Reef Lagoon (GBRL), though this contribution is difficult to quantify. It may also be important in driving the redistribution of phosphorus in the water column. The availability of nitrogen to drive offshore primary production in the GBRL may thus depend in large part upon the production and transport of *Trichodesmium*. Here, we describe a physiologically-based model of *Trichodesmium* production and nitrogen fixation which has now been incorporated into the eReefs marine modelling suite.

2. MODEL DESCRIPTION

2.1. Carbon, nitrogen and phosphorus reserves

The elemental ratios N:P:C:Chl in *Trichodesmium* colonies are allowed to vary. It is assumed that each cell contains a minimum structural component of each nutrient (maintained at the Redfield ratio) plus an extra reserve of each nutrient that can be used for growth and chlorophyll production. Note that the assumption that the Redfield C:N:P ratio represents the minimum structural P store relative to C probably considerably over-estimates structural P requirements.

2.2. Growth

The growth rate of *Trichodesmium*, μ_{Tricho} (d^{-1}) is given by:

$$\mu_{Tricho} = \mu_{\max\_Tricho} N_{res} I_{res} P_{res} T_{factor} \quad (1)$$

where $\mu_{\max\_Tricho}$ is the maximum daily growth rate (approximately 0.27 d 1 at a reference temperature of 20oC under current CO2 conditions according to the results of Hutchins et al. 2007), T_{factor} is an Arrhenius function of temperature, I_{res} is the energy reserve available per colony as a proportion of the maximum. Similarly, N_{res} and P_{res} are the non-structural intracellular nitrogen and phosphorus reserves, normalised to the maximum reserve (i.e. ranging between 0 and 1).

2.3. Nitrogen uptake and nitrogen fixation

Trichodesmium, like other nitrogen-fixing cyanobacteria, have the ability to use nitrogen from a variety of sources. In addition to taking up ammonium and nitrate from the water column, such cyanobacteria can fix N_2 and use some forms of dissolved organic nitrogen (DON) (urea and possibly some amino acids Flores and Herrero 2005).

The proportion of dissolved organic nitrogen that is present in these directly available forms in the GBRL has not been quantified, but is probably small. In this model, we assume that DON is not available to *Trichodesmium*.

Of the remaining forms of nitrogen present in the water column, *Trichodesmium* will use whichever available form has the lowest energy requirement for assimilation: NH_4^+ in preference to NO_3^- and either of these in preference to N_2.When NH_4^+ is available, assimilation of other forms of nitrogen is suppressed (Flores and Herrero 2005).

We allow *Trichodesmium* a variable intracellular nitrogen reserve store, with a preference for NH_4^+ over NO_3^- uptake, thus:

$$NH4uptake = K_{NH4}(1 - N_{res})c \quad (2)$$

(where NH4uptake is in mg N m^{-3} s^{-1}) and

$$NO3uptake = max(0, K_{NO3}(1 - N_{res})c - NH4uptake) \quad (3)$$

where NO3uptake is in mg N m^{-3} s^{-1}, c is the concentration of *Trichodesmium* colonies in the water (colonies m^{-3}), given by $c = \frac{Tricho_N}{m_{Tricho\_N}}$ where $Tricho_N$ represents the structural nitrogen store of *Trichodesmium* in the water (mg N m^{-3}) and m_{Tricho_N} is the number of milligrams of nitrogen per *Trichodesmium* colony.

K_{NH4} is the rate of transfer of NH_4 across the cell wall (mg N $cell^{-1}$ s^{-1}) and K_{NO3} is the rate of transfer of NO_3 across the cell wall (mg N $cell^{-1}$ s^{-1}), given by $K_{NH4} = \varphi_{Tricho} D_{NH4} NH4$ and and $K_{NO3} = \varphi_{Tricho} D_{NO3} DIN$ where NH4 is the concentration of NH_4^+ in the water (mg N m^{-3}), NO3 is the concentration of NO_3^- (mg N m^{-3}), D_{NH4} is the molecular diffusivity of NH_4^+ (m^2 s^{-1}), D_{NO3} is that of NO_3^- (m^2 s^{-1}) and φ_{Tricho} is the distance for diffusive transfer (m $cell^{-1}$), defaulting to the spherical approximation of 4 π times the radius of the cell.

Where the extracellular DIN concentration (i.e. NO3+NH4) falls below a minimum (DINcrit, typically 0.3 to 1.6 µmol L 1 (i.e. 4x10-3 to 2x10-2 mg N m 3) , Oliver et al. 2012), nitrogenase is produced to allow fixation of N_2. While we could attempt to simulate internal nitrogenase supplies or their activity (following, for example, the detailed physiological model of Stephens et al. 2003), we adopt a simpler approach and assume that nitrogenase becomes available whenever ambient DIN falls below the value of DIN_{crit} and energy and phosphorus are available to support nitrogen uptake:

$$N2uptake = \begin{cases} \max\left(K_{N2}\left(1 - N_{res}\right)c - NH4uptake - NO3uptake, 0\right), & DIN \le DIN_{crit} \text{ and } I_{res} > 0 \text{ and } P_{res} > 0 \\ 0, & \text{otherwise} \end{cases} \quad (4)$$

where $K_{N2} = \varphi_{Tricho} D_{N2} N2$, $N2uptake$ is in mg N m^{-3} s^{-1}, $N2$ is the concentration of N_2 dissolved in the water, assumed to be in equilibrium with the atmosphere and approximated as $2x10^4$ mg N m^{-3} (a value appropriate to fresh water at 20°C and 1000 kPa air pressure), D_{N2} is the diffusivity of N_2 (3.6×10^{-9} $m^2 s^{-1}$ in fresh water at 20°C).

The rate of change of storage of nitrogen by *Trichodesmium* (in excess of the minimum storage required to support the number of cells present at the Redfield C:N:P ratio) is given by:

$$\frac{dN_{Tricho\_R}}{dt} = NH4uptake + NO3uptake + N2uptake - \mu_{Tricho} Tricho_N \quad (5)$$

where $Tricho_N$ is the structural nitrogen store of *Trichodesmium* (i.e. the minimum store required to maintain a Redfield C:N:P ratio).

2.4. Micronutrient requirements

Micronutrients, notably including iron and molybdenum, are also required for nitrogenase production and nitrogen fixation. Iron availability has been demonstrated to limit *Trichodesmium* growth and nitrogen fixation in offshore waters. Since EMS does not track iron nor simulate the iron cycle, and since iron is rarely included in water quality monitoring, we do not include this limitation in our model, and will instead rely on phosphorus to provide a reasonable proxy for iron availability. This may be an acceptable approximation, as there is a suggestion that cyanobacteria can take up iron and other minerals quickly and store them for later use when they are available for short periods (Donnelly et al. 1997).

2.5. Light and energy requirements

Assimilation of nitrogen by nitrogen fixation is much more energetically expensive (8 mol ATP per mol N assimilated) than uptake from dissolved ionic sources of inorganic nitrogen (1 mol ATP per mol N). Assimilation of carbon requires 3 mol ATP per mol C. To maintain C:N at the Redfield ratio (106:16), cyanobacteria therefore require approximately 4.2 mol ATP per mol C assimilated when fixing nitrogen vs. 3.15 mol ATP per mol C assimilated when taking up nitrogen from ammonium or nitrate. Hence, nitrogen fixation should be expected to reduce carbon fixation by 33%, all else being equal.

The production of nitrogenase also requires carbon. In nitrogen-fixing cyanobacteria, nitrogenase typically accounts for approximately 10% of cellular protein. 60 to 75% of carbon in cyanobacteria is present in protein, so, overall, approximately 7% of fixed carbon must go to production and maintenance of nitrogenase in nitrogen-fixing cyanobacteria. Adding this to the above-mentioned reduction in carbon fixation, we arrive

at an estimated 40% increase in energetic cost of chlorophyll or carbohydrate production when nitrogen fixation is necessary.

A final factor is that *Trichodesmium*, unlike some other nitrogen-fixing cyanobacteria, do not have heterocysts (differentiated nitrogen-fixing cells) and, unlike a second group, fix nitrogen during the day rather than at night (Oliver et al. 2012). As a result, it is necessary for *Trichodesmium* to reduce photosynthesis and increase respiration in order to maintain a net zero or negative oxygen production rate to provide the reducing conditions that make nitrogenase activity possible. This can be expected to further reduce the *Trichodesmium* growth rate when nitrogen fixation is necessary.

The total net rate of accumulation of photons (stored in the form of ATP) by *Trichodesmium* is given by:

$$\frac{dI_{Tricho}}{dt} = I_{uptake} - \mu_{Tricho} Tricho_N \frac{r_{A\_I}}{r_{A\_N} M_{W\_N}} - R_I - Nfix \tag{6}$$

where $Tricho_N$ is the concentration of *Trichodesmium* in the water in mg N m^{-3}, $\frac{r_{A\_I}}{r_{A\_N} M_{W\_N}}$ is the minimum energy storage of 1 mg N m^{-3} of *Trichodesmium*, R_I represents the energy used for respiration (mol photons m^{-3}d^{-1}), I_{Tricho} is the number of moles of photons (stored as cellular ATP) in *Trichodesmium* per m^3 of water. The rate of uptake of photons per cubic metre, I_{uptake} (mol photons m^{-3}d^{-1}), is given by:

$$I_{uptake} = K_{I\_Tricho}(1 - I_{res})c \tag{7}$$

where K_{I_Tricho} is the maximum rate of absorption of photons per cell (mol photons colony^{-1}d^{-1}).

Since we assume a constant C:N ratio in the structural component, the rate of diversion of photons to nitrogen fixation, *Nfix* is given by:

$$Nfix = \begin{cases} I_{uptake}/3, & DIN < DIN_{crit} \\ 0, & \text{otherwise} \end{cases} \tag{8}$$

2.6. Photosynthesis and respiration

The energy loss associated with respiration is given by:

$$R_I = \mu_{\max\_Tricho} I_{Tricho} r \tag{9}$$

where *r* is a unitless respiration parameter (i.e. respiration as a proportion of the energy-limited growth rate).

As well as using energy, respiration results in a release of carbon to the surrounding water, while photosynthesis is associated with the uptake of carbon. Hence:

$$\frac{\partial DIC}{\partial t} = \left(R_I \mu_{\max\_Tricho} Tricho_N - \mu_{Tricho} Tricho_N \right) R_{w\_C} \tag{10}$$

where $\frac{\partial DIC}{\partial t}$ is the rate of change of dissolved inorganic carbon in the water column due to respiration and photosynthesis by *Trichodesmium* and R_{w_C} is the (Redfield) ratio between carbon and nitrogen (mg C (mg N)$^{-1}$).

Similarly,

$$\frac{\partial O}{\partial t} = \left(R_I \mu_{\max\_Tricho} Tricho_N - \mu_{Tricho} Tricho_N \right) R_{w\_O} \tag{11}$$

where $\frac{\partial O}{\partial t}$ represents the rate of change of oxygen in the water due to respiration and photosynthesis by *Trichodesmium* and R_{w_O} represents the corresponding ratio between oxygen and nitrogen (mg O (mg N)$^{-1}$).

2.7. Spectral absorption

In order to better simulate the light available to primary producers, a spectrally-resolved optical model is used. The optical model calculates the spectrally-resolved light field from a variety of absorption and scattering components in a number of wavelengths bands and hence the areal flux of photons available for uptake in each band (Baird et al., 2013). Within this model, the rate of light absorption due to *Trichodesmium*, K_{I_Tricho}, is calculated as a function of its absorption cross-section (a function of cell geometry and cellular chlorophyll concentration) and the scalar irradiance.

2.8. Chlorophyll production

The rate of change of intracellular chlorophyll concentration due to synthesis of chlorophyll attributable to *Trichodesmium* is given by:

$$\frac{dChl}{dt} = \begin{cases} Chl_{Tricho}\mu_{\max\_Tricho}(1-F_N)y_{Cfac\_Tricho}(1-I_{res}), & PN_{\max} < \dfrac{2.11Chl_{Tricho}}{c} \\ 0, & \text{otherwise} \end{cases} \quad (12)$$

where PN_{max} is the maximum intracellular reserve of nitrogen, Chl_{Tricho} is the intracellular concentration of chlorophyll in *Trichodesmium* (mg Chl m^{-3}), y_{Cfac_Tricho} is a dimensionless factor quantifying the incremental benefit of adding chlorophyll to photon absorption (Baird et al., 2013). The conditional statement prevents C:Chl ratios from dropping below 12. F_N is a factor representing the proportion of fixed carbon that goes to nitrogenase production.

$$F_N = \begin{cases} 0.07, & DIN > DIN_{crit} \\ 0, & \text{otherwise} \end{cases} \quad (13)$$

where DIN_{crit}, as mentioned above, is a critical DIN threshold below which nitrogenase is produced. Chlorophyll production and cell division by *Trichodesmium* otherwise follows Baird et al. (2013).

2.9. Buoyancy

Trichodesmium colonies are often seen floating at the surface of the water. Cells contain gas vacuoles, which provide a baseline positive buoyancy, but become ballasted with carbohydrates as carbon is accumulated due to photosynthesis (Villareal and Carpenter 2003). It has been suggested (Karl et al. 1992) that the resulting diel vertical migration of *Trichodesmium* colonies allows uptake of phosphorus at depth, so that *Trichodesmium* contribute substantially not only to the nitrogen budget, but also to the phosphorus budgets of oligotrophic surface waters. Villareal and Carpenter (2003) found some evidence to support this idea, in that positively buoyant colonies in the Gulf of Mexico (but not in tropical Australian waters) were found to have average N:P ratios considerably lower than negatively buoyant colonies (43.5 vs. 87.0).

Collapse of gas vesicles occurs at pressures of 1200-3700 kPa (Villareal and Carpenter 2003). Such pressures do not occur above 100 m depth in the water column, so gas vesicle collapse is not likely to be relevant in the Great Barrier Reef Lagoon and were therefore not included in the model.

Changes in the buoyancy of *Trichodesmium* are simulated as a function of the carbohydrate store, which is assumed to co-vary linearly with I_{res}.

$$\rho_{Tricho} = \rho_{\min} + I_{res}(\rho_{\max} - \rho_{\min}) \quad (14)$$

where ρ_{Tricho} is the density (g m^{-3}) of *Trichodesmium* colonies, and $\rho_{\max}$ and $\rho_{\min}$ are parameters controlling the maximum and minimum densities. Carbon fixed in excess of this limit may be exuded as extracellular mucous. Values for these parameters can be derived from the data presented by Villareal and Carpenter (2003).

Stokes' law is then applied to determine the rising or sinking rate as a function of density and colony size. Walsby (1978) found *Trichodesmium* colonies in three forms: spherical colonies 7-10 µm wide, tufts 8-21 µm wide and flat, fusiform filaments 11 µm wide, while Walsby (1978) reports floating and sinking velocities in the range -0.8 to 0.8 mm/s. In calculating an appropriate range for *Trichodesmium* colony densities, we assume spherical colonies.

When floating as a surface scum, the physics and chemistry of cyanobacterial blooms is complex and cannot be accurately represented simply by simulating the dynamics as if the cyanobacteria were simply mixed into a thin surface layer. An accurate model of surface blooms would need to consider direct wind advection (e.g. Wang et al. 2008), re-entrainment from the surface as a function of shear stress (Webster and Hutchinson 1994), the possible damping effects of a surface film layer on wave action (Milgram 1998) and the impacts of wave action on colony develeopment, the possible effects of the film layer on transfer of gases across the surface, and, if the scum is thick, the development of strong redox, carbon and nutrient gradients within this layer (Ibelings and Maberly 1998). Typically, *Trichodesmium* surface blooms are thin enough that some of these effects are negligible; however the physical dynamics of advection and entrainment of surface blooms should be considered as an avenue for model development.

2.10. Colony formation

Colony formation provides two advantages. First, colonies are believed to enhance nitrogen fixation by providing a region of low oxygen in the centre of colonies, while photosynthesis continues at the surface. Second, it enhances buoyancy-controlled vertical movement by increasing the effective particle size of *Trichodesmium*. Villareal and Carpenter (2003) found colony sizes (by mass) varied by a factor of 8, but not in a predictable manner. The model presented here assumes a constant colony size.

2.11. Grazing and cyanophages

In this first version of the *Trichodesmium* model, the zooplankton grazing term follows the approach taken for phytoplankton in EMS (Wild-Allen 2013), in which grazing depends on random encounters and is a function of zooplankton and phytoplankton concentrations and zooplankton swimming speed. In reality, the use of *Trichodesmium* by copepods as a physical substrate (O'Neil 1998), if common, must considerably enhance grazing rates. O'Neil (1998) demonstrated this in grazing experiments in Caribbean waters, and suggested that *Macrostella gracilis* plays an important role in bringing the nutrients fixed by *Trichodesmium* into the food-web. O'Neil (1998) measured grazing efficiencies averaging 21% and ingestion rates of up to 0.134 μG (μg C^{-1} h^{-1})$^{-1}$. It has been suggested (McKinnon, *pers. comm.*) that grazing on *Triochodesmium* in Great Barrier Reef waters in minimal, so grazing efficiency will be an interesting parameter for exploration.

Cyanophages populations are not directly simulated. Instead, we apply a quadratic mortality term, reflecting the fact that infection (and subsequent lysis) by cyanophages is more likely as populations increase. In natural populations of *Synechoccus*, phage numbers were found to increase dramatically once host populations reached a critical threshold of between 1000 and 10000 cells mL^{-1}. Hewson et al. (2004), however, noted that in the tuft colonies formed by *Trichodesmium*, transmission between trichomes and cells is less likely to be constrained by population. In our model,

$$m = \begin{cases} \left(Tricho - Tricho_{crit}\right)^2 m_{Q\_T} T_{factor}, & Tricho > Tricho_{crit} \\ 0, & otherwise \end{cases} \quad (15)$$

where m_{Q_T} is a quadratic mortality term , and $Tricho_{crit}$ is a critical threshold for *Trichodesmium* attack by phages (mg N m^{-3}), with a default value of zero.

3. CONCLUSIONS

We have described a novel, physiologically-based model of *Trichodesmium* growth, buoyancy and nitrogen fixation. With few exceptions, the parameters used in the model have been derived from the literature describing empirical observations in the field, which will allow the hypothesised important role of *Trichodesmium* in the nitrogen budget of the Great Barrier Reef Lagoon to be tested through simulations. The model described here has been incorporated into a complex, process-based, hydrodynamic and biogeochemical model of the GBRL, which will facilitate informed management decisions for the future of this important environmental asset. Results of incorporation of the *Trichodesmium* model into the GBRL model are not yet available.

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