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Phosphorus dynamics of the tropical and subtropical north Atlantic: *Trichodesmium* spp. versus bulk plankton

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ABSTRACT: Nitrogen fixing organisms such as *Trichodesmium* spp. are abundant in the oligotrophic tropical North Atlantic Ocean, where microplankton (including other diazotrophs) are more likely to be phosphorus (P) than nitrogen (N) limited. Thus, understanding the ability of different functional groups in the plankton to compete for P in this area is important for understanding their relative success. The uptake of phosphate by *Trichodesmium* spp. colonies and bulk water plankton was measured using $^{33}PO_4^{3-}$ over a range of concentrations, and kinetic parameters were determined. Nano- and pico-plankton present in bulk water samples have a K_s that is nearly 30 times lower than that of *Trichodesmium* spp. While chl *a*-normalized alkaline phosphatase activity (APA) in bulk water was an order of magnitude greater than in *Trichodesmium* spp., *Trichodesmium* spp. contributes substantially to total APA in the water. *Trichodesmium* spp. is outcompeted for dissolved inorganic P (DIP), but colonies can satisfy their P needs by supplementing DIP uptake with P cleaved from dissolved organic P (DOP) via alkaline phosphatase.

KEY WORDS: Phosphorus · Phosphate · Nitrogen fixation · *Trichodesmium* · North Atlantic

INTRODUCTION

Phosphorus (P) has a very long residence time in the oceans (Codispoti 1989), even though estimates have been recently revised downwards due to new analyses (Benitez-Nelson 2000). The cycling of this macronutrient has long been viewed as primarily controlled by chemical processes occurring on geological time scales, with the conversions that happen in the biological realm being incidental (Tyrell 1999, Benitez-Nelson 2000). This stems from the common view that biological productivity of the world's oceans is primarily nitrogen (N) limited, with changes in P cycling (Benitez-Nelson 2000) or N inventories being tempered through the regulation of nitrogen fixation and denitrification (Michaels et al. 2001). However, certain areas of the globe are now thought to be P limited (e.g. the Mediterranean, Thingstad et al. 2005); thus the study of P dynamics in these areas is essential.

Trichodesmium spp. is a nitrogen fixing, colony forming cyanobacteria that occurs in many areas of the ocean where warm, calm waters and oligotrophic conditions prevail (Capone et al. 1997). Colonies can take on either the tuft formation (parallel alignment of trichomes) or the puff formation (radially arranged trichomes). The diazotrophic nature of *Trichodesmium* spp. ensures that it is never limited by N, and thus other nutrients are important in regulating growth and nitrogen fixation. Both P and Fe have been suggested as limiting to diazotrophs, but it appears most likely that different nutrients may limit nitrogen fixers in different areas of the ocean. High concentrations of Fe from large fluxes of dust from the African continent (Wu et al. 2000) and high densities of nitrogen fixing organisms such as *Trichodesmium* spp. (Carpenter et al. 2004, Capone et al. 2005) create conditions conducive to P limitation in the tropical and subtropical North Atlantic (Wu et al. 2000, Sañudo-

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Wilhelmy et al. 2001). Studies show that both the bulk water plankton (made up in large part by heterotrophic bacteria and the cyanobacteria *Prochlorococcus* spp. and *Synechococcus* spp. [Li et al. 1992]) and *Trichodesmium* spp. are P limited in the North Atlantic (Cotner et al. 1997, Sañudo-Wilhelmy et al. 2001, Ammerman et al. 2003, Krauk et al. 2006). The apparent limitation by P of these various groups means that they must compete with each other for P from both the dissolved inorganic (DIP) and organic (DOP) pools. Both picoplankton and *Trichodesmium* spp. can access the DIP and DOP pools of P through P transport enzymes and alkaline phosphatase. In addition, basic local alignment search tool (BLAST) searches have found sequences in the genome of *Trichodesmium erythraeum* IMS 101 for phosphonate transport and metabolism proteins, indicating that *Trichodesmium* spp. may be able to exploit this often overlooked component of DOP (genome.ornl.gov/microbial/tery, Dyhrman et al. 2006).

How, exactly, a *Trichodesmium* spp. colony is able to acquire enough P to fulfill its cellular requirements when it grows in areas with such low PO_4^{3-} concentrations has been an issue of debate for years, with some suggesting that colonies might migrate towards the phosphocline when P-depleted to take up large amounts of P and then return to the surface (Karl et al. 1992). However, if *Trichodesmium* spp. can successfully compete for either DIP or DOP, it may be able to acquire the necessary P for growth without migration to the phosphocline.

To assess the ability of *Trichodesmium* spp. to compete with bulk plankton for P in a P limited system, we measured PO_4^{3-} uptake kinetics and alkaline phosphatase activity for both sample types in the subtropical and tropical western North Atlantic in March 2004.

MATERIALS AND METHODS

Sample collection. Experiments were performed aboard the RV 'Endeavor' in March 2004 on a southeast transect from about 30° N, 65° W down to 10° N, 50° W (Fig. 1). Samples were collected by towing a 0.25 m, 202 mm mesh net at a depth of 15 to 20 m for about 10 min at a time. Colonies were found in both the puff and tuft formations, with puffs outnumbering tufts. Colonies were picked out of the tow sample using a plastic inoculating loop and placed into filtered seawater to rinse. The colonies were then picked out of the rinse and placed in bottles used for different assays. Efforts were made to place the different colony conformations into assays at approximately the same abundance that they were found in the tow. Colonies were not obtained at all stations, particularly those at the northern end of the transect. Bulk plankton was collected from either a clean underway seawater system or from near the surface (<2 m depth) sampled by a Niskin bottle on a CTD rosette system.

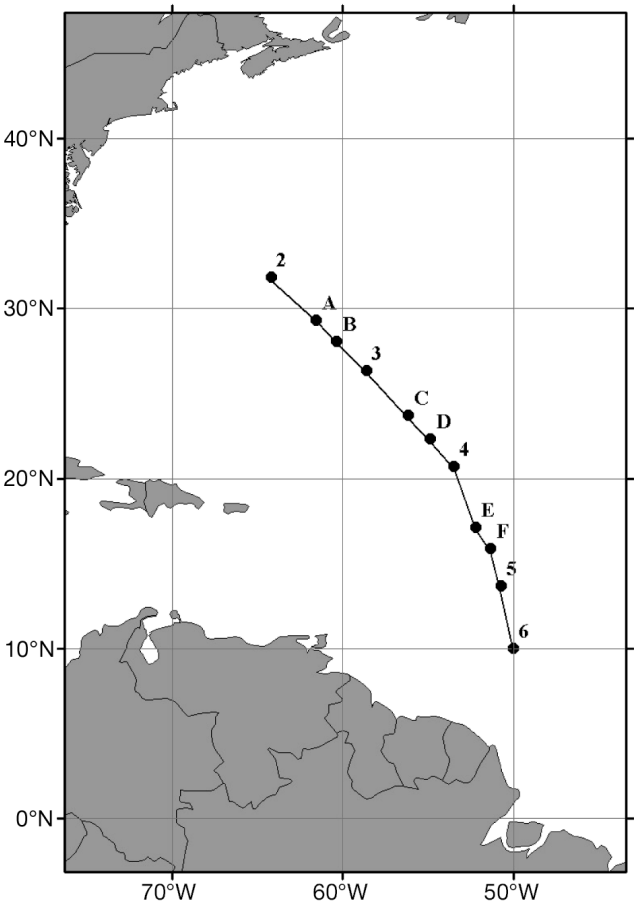

Fig. 1. Station locations in the subtropical and tropical North Atlantic

PO_4^{3-} uptake. Samples (50 ml) of bulk seawater or filtered seawater containing 10 *Trichodesmium* spp. colonies were placed in 60 ml acid washed polycarbonate bottles with 0.5 to 2 µCi of $^{33}PO_4^{3-}$ and incubated in 25% light on deck incubators for 60 to 90 min. Incubations were filtered onto polycarbonate filters, 8 µm for *Trichodesmium* spp. colonies and 0.2 µm for bulk seawater samples. Incubation bottles were rinsed 3 times with 0.2 µm filtered seawater, the rinse poured over the filters, with one final filtered seawater rinse of the filter towers before the filters were placed into 7 ml plastic scintillation vials. Activity of ^{33}P was measured on board in a scintillation counter after addition of 5 ml scintillation cocktail. Experiments conducted on this cruise and on previous cruises that showed DIP uptake in *Trichodesmium* spp. is linear for the first 60 to 90 min. Other studies have shown that DIP uptake in bulk samples of seawater is linear for many hours (Björkman et al. 2000).

The Michaelis-Menten equation is used to describe the uptake kinetics of nutrients. By fitting the equation $V = V_{max} \times S(K_s + S)^{-1}$ to a plot of PO_4^{3-} concentration (S) in an incubation versus the PO_4^{3-} uptake rate (V) at that concentration, one can solve for the rate of maximal uptake (V_{max}) and the half saturation constant (K_s). To create kinetic curves, 0 to 1 µM of cold PO_4^{3-} was added to incubations, followed immediately by radiolabeled PO_4^{3-} addition. Samples were then treated as described above. SigmaPlot was used to directly fit the Michaelis-Menten equation to the data and extract V_{max} and K_s (K_s was corrected for the amount of DIP measured in surface water). It has been recently shown that a significant amount of phosphorus in a colony is sorbed to the outside of the cells, and washing sorbed P from the outside of the cells is important when measuring actual P uptake with $^{33}PO_4^{3-}$ (Sañudo-Wilhelmy et al. 2004). To control for this abiological adsorption of phosphorus, a killed control was always conducted with addition of 1 ml of glutaraldehyde to measure abiological adsorption to colonies, and calculations for P uptake were corrected for this. Uptake of the radioisotope in killed controls of *Trichodesmium* spp. was 8% (on average) of the uptake of ^{33}P into live colonies.

Alkaline phosphatase activity. The PO_4^{3-} moiety is cleaved from DOP at the cell surface and taken up as inorganic PO_4^{3-}, and thus will not be accounted for in measurements of PO_4^{3-} uptake with respect to ambient PO_4^{3-} concentration. It is therefore important to measure the activity of alkaline phosphatase separate from PO_4^{3-} uptake to assess the potential for uptake of phosphate from the DOP pool.

The method described by Ammerman (1993) was used to measure APA. Briefly, 250 ml samples of surface seawater or 30 colonies of *Trichodesmium* spp. in unfiltered surface seawater were incubated with 100 nM methylumberiferone (MUF-P). Alkaline phosphatase cleaves the PO_4^{3-} moiety from the molecule, causing it to fluoresce. Samples were incubated in on-deck incubators at 25% light and the increase in fluorescence of MUF was measured over the course of the day, usually over a 6 to 7 h period, using a Turner 10-AU fluorometer with a long WL oil lab filter kit. APA was calculated using the linear portion of the slope of MUF fluorescence versus time, relative to a 100 nM MUF standard, and the concentration of DOP in the water. For assays on *Trichodesmium* spp., the rate of APA measured in seawater was subtracted from the activity of *Trichodesmium* spp. plus surface seawater to obtain activity of *Trichodesmium* spp. alone. Experiments were conducted in this manner because in previous experiments, we have seen that filtering seawater can increase activity relative to unfiltered water, possibly due to cell breakage and release of the phosphatase enzyme.

Chl *a* and nutrient analyses. Chl *a* concentrations were determined by filtering 1 l of seawater onto a GF/F glass fiber filter, extracting the chlorophyll with acetone for 24 h, then reading the sample on a fluorometer set to detect chl *a* and comparing it to a known standard. Chlorophyll from colonies of *Trichodesmium* spp. was also extracted in acetone and measured on a fluorometer after 24 h. Surface samples for DIP concentration were collected in acid washed plastic vials and measured with the MAGIC method (Karl & Tien 1992). Samples were concentrated by a factor of 6, making the limit of detection 5 nM. Total dissolved phosphorus (TDP) was measured on unfiltered samples (as PP was assumed to be <10% of total P) using the high temperature combustion and acid hydrolysis method of Solorzano & Sharp (1980). DOP was calculated by subtracting DIP from TDP.

RESULTS

DIP and DOP concentrations in this area of the North Atlantic Ocean were found to be very low at this time of year, with DIP averaging 0.04 µM, while DOP concentrations were almost an order of magnitude higher at 0.11 µM (Table 1). Chl *a* showed about a 10-fold range of concentrations along the transect, from 0.018 to 0.22 µg l^{-1}, whereas *Trichodesmium* spp. chl *a* content was 8 to 27 µg $colony^{-1}$.

Chl *a*-normalized APA in bulk water was similar among most stations. However, Stn 3 showed an extreme rate of 83.9 nmol P mg chl a^{-1} h^{-1}, much higher than at the other stations. On average, bulk water APA was 19.4 ± 32.1 nmol P µg chl a^{-1} h^{-1}. APA for *Trichodesmium* spp. was measured at 3 stations, and the activity measured averaged 5.9 ± 3.8 nmol P µg chl a^{-1} h^{-1}. When comparing average *Trichodesmium* spp. APA to bulk water APA, chl *a*-specific bulk water APA was 4 times greater than that of *Trichodesmium* spp. over the entire region studied. However, if the high value from Stn 3 is removed, they are nearly the same.

The chl *a*-normalized uptake of PO_4^{3-} at ambient concentrations in bulk water samples measured with ^{33}P was nearly a factor of 3 greater than uptake from the DOP pool (as measured from APA), while DIP uptake in *Trichodesmium* spp. was an order of magnitude less than APA.

Phosphate uptake kinetic curves were determined for bulk water at 2 stations (B and C) and *Trichodesmium* spp. at 2 stations (5 and 6), with 2 curves produced at Stn 6. An example of each can be seen in Fig. 2. V_{max} averaged 12.2 ± 2.1 nmol P µg chl a^{-1} h^{-1} for bulk samples and 10.3 ± 4.7 nmol P µg chl a^{-1} h^{-1} for *Trichodesmium* spp. (Table 2). K_s of bulk plankton was 0.015 µM at both stations where it was measured, while

Table 1. Concentrations of chl *a*, DIP and DOP in the North Atlantic Ocean and DIP uptake and alkaline phosphatase activity (APA) of bulk water samples and *Trichodesmium* spp. colonies at ambient DIP and DOP concentrations. At Stn 6, bulk water and *Trichodesmium* spp. PO_4^{3-} uptake rates were determined twice. Tricho: *Trichodesmium* spp.

Stn	DIP (µM)	DOP (µM)	Bulk chl *a* (µg l^{-1})	Tricho chl *a* (µg $colony^{-1}$)	Bulk APA (nmol P µg chl a^{-1} h^{-1})	Tricho APA (nmol P µg chl a^{-1} h^{-1})	Bulk PO_4 uptake (nmol P µg chl a^{-1} h^{-1})	Tricho PO_4 uptake (nmol P µg chl a^{-1} h^{-1})
2	0.05	0.17	0.121		17.6		25.0	
A	0.01	0.18	0.22		1.5		2.8	
B	0.02	0.09	0.21				7.1	
3	0.02		0.018	0.015	83.9		61.1	0.02
C	0.01	0.06	0.026		3.9		53.8	
D	0.01	0.07	0.035				48.6	
4	0.08			0.027		4.5		0.51
E	0.04	0.10	0.051		6.5		154.9	
F	0.03	0.12	0.039				74.4	
5	0.06			0.019		3.1		0.27
6	0.07		0.128	0.008/0.008	3.1	10.3	69.5/43.8	1.03/0.62
Average	0.04	0.11	0.16	0.015	19.4	5.9	54.1	0.53

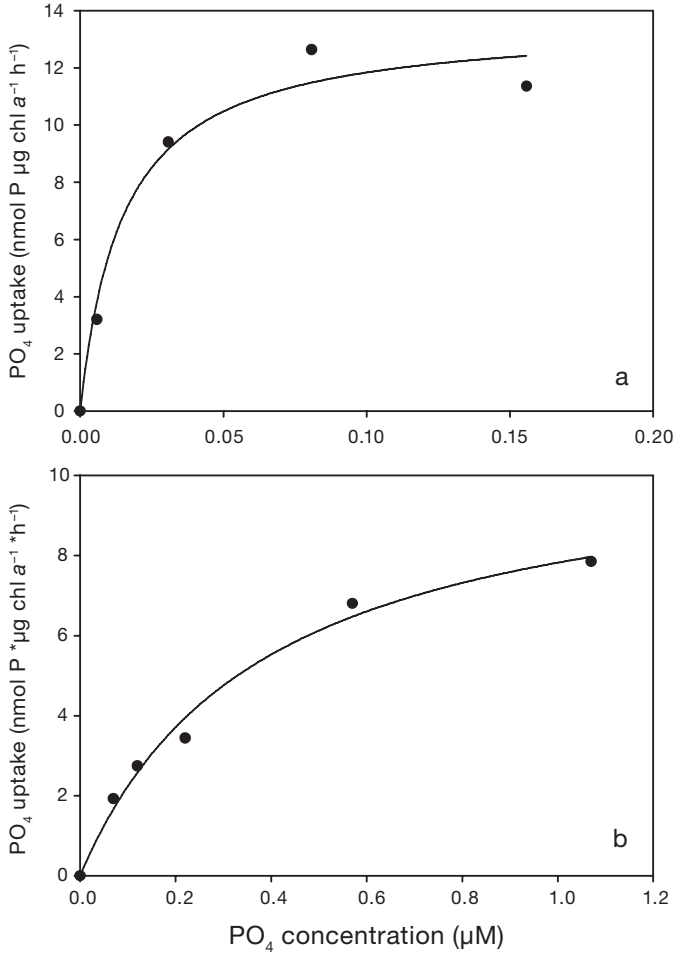

Fig. 2. Examples of kinetic curves for (a) bulk water samples (Stn B) and (b) *Trichodesmium* spp. colonies (Stn 6). PO_4^{3-} concentration represents amount of cold PO_4^{3-} added to incubations plus ambient PO_4^{3-} concentration in surface water. Note different scales on *x*- and *y*-axes

K_s of *Trichodesmium* spp. was 0.78 ± 0.37 µM on average, 50 times greater than that of bulk plankton (Table 2). The affinity of bulk plankton and *Trichodesmium* spp. for PO_4^{3-} can be calculated as $V_{max} \times K_s^{-1}$ (also known as a), and was 0.81 and 0.016 l µg chl a^{-1} h^{-1}, respectively.

DISCUSSION

Based on previous studies (Cotner et al. 1997, Rivkin & Anderson 1997, Obernosterer et al. 2003) and rapid PO_4^{3-} pool turnover times of about 10 h in the surface waters measured during our cruise in March 2004 (data not shown), the area in the western North Atlantic from 30° to 10° N appears to be strongly P limited. The relatively high surface concentrations of Fe (Wu et al. 2001), comparisons of nitrogen fixation rates with colony P content (Sañudo-Wilhelmy et al. 2001) and particulate N:P ratios that are very high (Krauk et al. 2006), have led others to conclude that P exerts a major control on *Trichodesmium* spp. growth specifically, and diazotroph growth in general, in the tropical and subtropical North Atlantic. Dyhrman et al. (2002) also concluded that *Trichodesmium* spp. colonies in this region are severely P stressed, by using an ELF assay that visualizes P-stressed trichomes. Our results from *Trichodesmium* spp. populations in this area also point to P limitation. V_{max} values are 11 and 7 times greater than those found in the North Pacific Subtropical Gyre and off the north coast of Australia (J. A. Sohm et al. unpubl. data), areas that may be less P limited than the North Atlantic. Thus, competition for phosphorus among the planktonic organisms in the North Atlantic may be a defining feature of this ecosystem.

Table 2. V_{max}, K_s, and α for bulk water and *Trichorichodesmium* spp. samples (values determined twice at Stn 6). Parameters found by fitting the Michaelis-Menten equation to data. α: $V_{max} \times K_s^{-1}$

Stn	V_{max} (nmol P µg chl a^{-1} h^{-1})	K_s (µM)	α (l µg chl a^{-1} h^{-1})
Bulk plankton			
B	13.6	0.015	0.91
C	10.7	0.015	0.71
Trichodesmium spp.			
5	5.5	0.85	0.006
6	10.8	0.38	0.028
6	14.8	1.1	0.013

Chl *a*-normalized uptake rates of DIP and alkaline phosphatase activity were both higher in bulk plankton than in *Trichodesmium* spp., as was the calculated V_{max}. It is important to recognize that a portion of the activities measured in bulk samples are carried out by heterotrophic bacteria, and thus that these organisms are not represented in the chl *a* measurements. This problem can be overcome by estimating volumetric rates (Table 3), and it can be seen that the patterns still hold.

While there are measurements of P uptake and APA in different areas of the Atlantic for either bulk water plankton or *Trichodesmium* spp., ours is the first study to directly compare these enzyme activities in both bulk samples of water and *Trichodesmium* spp. Donald et al. (2001) measured P uptake by bulk plankton along a transect at 20° W between 57.5° and 37° N, and found rates of 0.42 to 1.7 nM h^{-1}, which are comparable to but less than the average volumetric P uptake found in our study of 4.8 nM h^{-1} (Table 3). Maximal PO_4 uptake found at stations in the Sargasso Sea near Bermuda was 0.78 nM h^{-1} in August and 0.82 nM h^{-1} in March (Cotner et al. 1997), less than the ambient uptake rates found in our study. However, P uptake in our study was generally lower at the more northern stations where Cotner et al. (1997) collected their data, and comparable to the rates found in their study. Maximal alkaline phosphatase activity found in the same study was 1.39 nM h^{-1} in August and 2.7 nM h^{-1} in March. While this is higher on average than the rates that we found (0.65 nM h^{-1}), the APA observed at the Bermuda Atlantic Time Series station (near where the Cotner et al. [1997] data was collected) was 2.13 nM h^{-1}, which is in line with results from Cotner et al. (1997).

Trichodesmium spp. APA observed in the present study is within the range of activities found for *Trichodesmium* spp. in waters north of Australia (0.65 to 13.1 nmol P µg chl a^{-1} h^{-1}), a location that has much higher concentrations of DOP than found in this study (Mulholland et al. 2002). APA reported for *Trichodesmium* spp. in the southwest North Atlantic in late May was found to range from 0.03 to 0.24 µmol MUF-P hydrolyzed µg chl a^{-1} h^{-1} (Mulholland et al. 2002), which was 1 to 2 orders of magnitude higher than the rates found in our study. Another study of *Trichodesmium* spp. APA in the Red Sea, which used the substrate *p*-nitrophenylphosphate, found activities of 2.4 to 11.7 µmol *p*-nitrophenylphosphate hydrolyzed µg chl a^{-1} h^{-1} (Stihl et al. 2001). However, this data represents maximal uptake rates, as saturating substrate concentrations were added and the experiments were conducted at 37°C. While these rates are not directly comparable, they suggest that *Trichodesmium* spp. in the western tropical Atlantic near the Caribbean and possibly in the Red Sea are substantially more P-stressed than colonies observed in our study.

Only 1 study to date has measured both DIP and DOP dynamics in *Trichodesmium* spp., and this data set is limited. McCarthy & Carpenter (1979) measured PO_4^{3-} uptake kinetics of *Trichodesmium* spp. at 1 station in the Central Atlantic at 30° N and APA at 2 stations on the same transect. This early work demonstrated the ability of *Trichodesmium* spp. to gain a large part of its phosphorus quota from the DOP pool. APA obtained from 2 experiments, measured using the 3-0 methylumbelliferyl phosphate method, was 2 orders of magnitude higher (170 and 300 nmol P µg chl a^{-1} h^{-1}) than found in the present study. The K_s reported for *Trichodesmium* spp. (9 µM) was far greater than observed in our study. A subsequent

Table 3. Average volumetric rates of DIP uptake and APA for bulk plankton and *Trichodesmium* spp., assuming 1 colony l^{-1} (Carpenter et al. 2004), and percentage of total uptake or activity for which either group is responsible

	DIP uptake (nM h^{-1})	APA (nM h^{-1})	15% APA[a] (nM h^{-1})	% of total DIP uptake	% of total APA
Bulk plankton	4.8 ± 4.2	0.65 ± 0.74	0.10	99.9	89.5
Trichodesmium spp.	0.0067 ± 0.0042	0.076 ± 0.028	0.011	0.1	10.5

[a]Column shows APA if only 15% of DOP is bioavailable, the upper limit found by Björkman & Karl (2003)

study of P uptake in exponentially growing batch cultures of *Trichodesmium* spp. isolated from the North Atlantic found a much lower K_s value of about 0.4 µM for both P replete and P deplete cells (Fu et al. 2005), very similar to the values found in our study. The doubling time for *Trichodesmium* spp. colonies in the North Atlantic based on PO_4^{3-} uptake alone was 5000 h, or 208 d (McCarthy & Carpenter 1979). A recent publication contends that this doubling time was too large by 3 orders of magnitude (Moutin et al. 2005). Close inspection does show that the PO_4^{-3} uptake values reported in the text (used to calculate the doubling time) differ by 3 orders of magnitude from the graph of PO_4^{3-} uptake kinetics. However, McCarthy & Carpenter (1979) became aware of this discrepancy soon after it was published, and state that the original values reported in the text are correct, while a symbol was misprinted on the *y*-axis of the graph of this data (J. McCarthy pers. comm.). Therefore, their results on the importance of DOP for *Trichodesmium* spp. should still be considered relevant.

Based on the K_s and affinity (α) values found in our study, *Trichodesmium* spp. cannot effectively compete for phosphate with smaller planktonic organisms in the upper water column. It does, however, have high rates of APA compared to DIP uptake. Thus we surmise that the DOP pool is very important to *Trichodesmium* spp. with respect to P acquisition, while for the nano- and picoplankton in the water, it may be merely a supplement. Very similar results were found in the central Baltic Sea where the heterocycstous cyanobacteria *Nodularia spumigena* and *Aphanizomenon* sp. occur (Nausch et al. 2004). In this area, when P limitation occurred in mid-summer, 91% of PO_4^{3-} uptake was carried out by the smallest size fractions (0.2 to 3 µm) while the >10 µm fraction, which included large amounts of cyanobacteria, was responsible for 42% of APA, indicating that DOP is a much greater source of P to heterocystous cyanobacteria in the Baltic Sea than DIP (Nausch et al. 2004). The importance of the DOP pool to *Trichodesmium* spp. was alluded to in a study of *Trichodesmium* spp. ultrastructure in sinking and rising colonies in the Caribbean (Romans et al. 1994). Sinking colonies were found at 25 m (a depth of low PO_4^{3-} concentrations) with large inclusions of polyphosphate. Presumably, *Trichodesmium* spp. would have had to access the DOP pool to accumulate these large amounts of intracellular P (Romans et al. 1994).

However, a very different result was obtained in a recent study on PO_4^{3-} uptake by *Trichodesmium* spp. in the South Pacific, near New Caledonia (Moutin et al. 2005). From P-specific PO_4^{3-} uptake data, the authors calculated that *Trichodesmium* spp. could achieve a growth rate of 0.1 d^{-1} at a PO_4^{3-} concentration of 9 nM. Thus, *Trichodesmium* spp. could coexist with smaller plankton by growing slowly and using only DIP (Moutin et al. 2005). Our data show a very different result. Assuming a colony P quota of 3.9 nmol (Carpenter 1983), PO_4^{3-} concentrations would have to be 0.15 µM to achieve a 0.1 d^{-1} growth rate, higher than DIP concentrations found in surface waters. Thus, in the subtropical and tropical North Atlantic, where our study was carried out, *Trichodesmium* spp. does not appear to be able to grow on DIP alone. Uptake of P from the DOP pool appears very important to growth.

It is important to consider that APA derived from the MUF-P method does not take into account the bioavailability of the DOP pool. Björkman & Karl (2003) estimate that 7 to 15% of DOP in the North Pacific is available to organisms. If a DOP bioavailability of 15% is assumed, the importance of DOP as a P source to *Trichodesmium* spp. is reduced (Table 3), but would still account for over 60% of P acquisition. DOP availability of 15% reduces the contribution of DOP in bulk plankton to a very low 2%.

To assess the volumetric contribution of *Trichodesmium* spp. to total uptake from the DIP and DOP pools, we assumed colony density in this area to be 1 colony l^{-1} (Carpenter et al. 2004) to evaluate what percentage of P from each pool might be incorporated into *Trichodesmium* spp. This was calculated by dividing ambient PO_4^{3-} uptake or APA of *Trichodesmium* spp. by the sum of *Trichodesmium* spp. and bulk seawater PO_4^{3-} uptake or APA. While virtually none of the DIP would be taken up by *Trichodesmium* spp. (0.1%), *Trichodesmium* spp. could be responsible for nearly 11% of the total uptake of DOP (Table 3). Therefore, *Trichodesmium* spp. contributes considerably to the turnover of the DOP pool, while the turnover of the DIP pool is carried out almost entirely by smaller organisms in the water. This is in agreement with measurements of size-fractionated P uptake in the Atlantic. In the northeastern Atlantic it was found that the smallest size fraction, 0.2 to 2 µm, was responsible for the bulk of the PO_4^{3-} uptake (58 to 88%, Donald et al. 2001). For a wide area of the central Atlantic, P uptake was also found to be greatest for the smallest organisms (Cañellas et al. 2000).

The half saturation constants (K_s) calculated for the picoplankton are about equal to the PO_4^{3-} concentrations found at those same stations: 0.02 µM PO_4^{3-} versus a K_s of 0.015 µM at Stn B, 0.01 µM PO_4^{3-} versus a K_s of 0.015 µM at Stn C. These organisms are therefore very well suited to take up DIP in this area, and are operating near their maximum uptake capacity. *Trichodesmium* spp., on the other hand, has a K_s of 0.78 µM, much greater than the average PO_4^{3-} concentration of 0.04 µM observed during our cruise (March 2004). Based on this data and the average V_{max}, *Tricho-*

desmium spp. is operating at 4 to 5% of maximum PO_4^{3-} uptake capacity at ambient PO_4^{3-} concentrations. Thus, *Trichodesmium* spp. is poised to take up pulses of high phosphate, should they occur. This finding is similar to that of Suttle et al. (1990), which showed that increasing proportions of DIP enter the larger size fractions as more P is added to Sargasso Sea water. At a PO_4^{3-} concentration of 0.04 µM, nearly all of the PO_4^{3-} (~99%) is taken up by the picoplankton. However, if a PO_4^{3-} pulse of 0.4 µM were to occur in these waters, about 5% of the PO_4^{3-} would enter the *Trichodesmium* spp. pool. At most, 15% of PO_4 could be incorporated into *Trichodesmium* spp. if PO_4 concentrations became high enough. As can be seen, at nominal densities of 1 colony l^{-1}, *Trichodesmium* spp. will not be a large contributor to PO_4^{3-} uptake even if concentrations increase; however, PO_4^{3-} would become an increasingly important component of total P acquisition by *Trichodesmium* spp. Conversely, at more extreme densities of *Trichodesmium* spp. as are sometimes encountered (Carpenter & Capone 1992), DIP uptake could be dominated by this phytoplankter.

Using the sum of average PO_4^{3-} uptake and APA, we can calculate the turnover time of *Trichodesmium* spp. colony P. Assuming a colony P content of 3.9 nmol (Carpenter 1983), the P turnover time is about 2 d, and doubling time is 1.4 d. This is well within estimates of colony doubling times based on C or N, which range from 1 to 2 d to >1 wk (Carpenter 1983, Carpenter & Romans 1991). This does, however, assume that all of the DOP pool is bioavailable to *Trichodesmium* spp. Using the estimate of Björkman & Karl (2003) of 7 to 15% DOP bioavailability, turnover of *Trichodesmium* spp. colony P from DIP and DOP would be 9 to 13.5 d, and a doubling time of 6.2 to 9.4 d. Even when taking the bioavailability of the DOP pool into account, *Trichodesmium* spp. appears to be able to double its colony P in about the same amount of time as C- or N-based estimates of doubling time (Carpenter 1983, Carpenter & Romans 1991). Thus, *Trichodesmium* spp. do appear to be able to acquire most or all of the necessary P for growth from the DIP and DOP pools. Slower growth by *Trichodesmium* spp. or, alternatively, reduced P quotas, would further decrease the doubling times of colony P.

Picoplankton and *Trichodesmium* spp. both appear to be P-limited or perhaps P-stressed in the subtropical and tropical North Atlantic, and thus the acquisition of P by these organisms is important to their growth. It appears that each has its own strategy to deal with this problem: picoplankton found in large numbers in bulk water samples have a high affinity for DIP and also the ability to derive some of P from the organic fraction; in contrast, *Trichodesmium* spp. cannot compete very successfully for inorganic PO_4^{3-} with smaller organisms in the water, but can obtain considerable amounts of P from the DOP pool. By utilizing this much larger pool, *Trichodesmium* spp. is able to coexist with picoplanktonic organisms in this area of P limitation.

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