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.

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

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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 south-east 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.

**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 \( V = V_{\text{max}} \times S/(K_s + S) \) 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 \( (V_{\text{max}}) \) and the half saturation constant \( (K_s) \). To create kinetic curves, 0 to 1 \( \mu \)M 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 \( V_{\text{max}} \) 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 \( ^{33}PO_4^{3-} \) (Sanudo-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 \textit{Trichodesmium} spp. was 8% (on average) of the uptake of \( ^{33}P \) into live colonies. The PO\(_4^{3-}\) moiety is cleaved from \( PO_4^{3-} \) to 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.

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 \textit{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 \textit{Trichodesmium} spp., the rate of APA measured in seawater was subtracted from the activity of \textit{Trichodesmium} spp. plus surface seawater to obtain activity of \textit{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.

**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 \( \mu \)M, while DOP concentrations were almost an order of magnitude higher at 0.11 \( \mu \)M (Table 1). Chl \( a \) showed about a 10-fold range of concentrations along the transect, from 0.018 to 0.22 \( \mu \)g l\(^{-1} \), whereas \textit{Trichodesmium} spp. chl \( a \) content was 8 to 27 \( \mu \)g 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 \( \mu \)g chl \( a \)\(^{-1} \) h\(^{-1} \). APA for \textit{Trichodesmium} spp. was measured at 3 stations, and the activity measured averaged 5.9 ± 3.8 nmol P \( \mu \)g chl \( a \)\(^{-1} \) h\(^{-1} \). When comparing average \textit{Trichodesmium} spp. APA to bulk water APA, chl \( a \)-specific bulk water APA was 4 times greater than that of \textit{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 \textit{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 \textit{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. \( V_{\text{max}} \) averaged 12.2 ± 2.1 nmol P \( \mu \)g chl \( a \)\(^{-1} \) h\(^{-1} \) for bulk samples and 10.3 ± 4.7 nmol P \( \mu \)g chl \( a \)\(^{-1} \) h\(^{-1} \) for \textit{Trichodesmium} spp. (Table 2). \( K_s \) of bulk plankton was 0.015 \( \mu \)M at both stations where it was measured, while...
Ks 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 PO4$_{3^-}$ can be calculated as $V_{max} \times Ks^{-1}$ (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 PO4$_{3^-}$ 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.
found rates of 0.42 to 1.7 nM h–1, which are 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. A subsequent 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 PO₄³⁻ 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 Kₛ reported for *Trichodesmium* spp. (9 µM) was far greater than observed in our study. A subsequent

<table>
<thead>
<tr>
<th>Stn</th>
<th>Vₘₐₓ (nmol P µg chl a⁻¹ h⁻¹)</th>
<th>Kₛ (µM)</th>
<th>α (l µg chl a⁻¹ h⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bulk plankton</td>
<td>13.6</td>
<td>0.015</td>
<td>0.91</td>
</tr>
<tr>
<td>C</td>
<td>10.7</td>
<td>0.015</td>
<td>0.71</td>
</tr>
<tr>
<td><em>Trichodesmium</em> spp.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>5.5</td>
<td>0.85</td>
<td>0.006</td>
</tr>
<tr>
<td>6</td>
<td>10.8</td>
<td>0.38</td>
<td>0.028</td>
</tr>
<tr>
<td>6</td>
<td>14.8</td>
<td>1.1</td>
<td>0.013</td>
</tr>
</tbody>
</table>

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 Vₘₐₓ. 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.

Table 3. Average volumetric rates of DIP uptake and APA for bulk plankton and *Trichodesmium* spp., assuming 1 colony l⁻¹

<table>
<thead>
<tr>
<th>DIP uptake (nM h⁻¹)</th>
<th>APA (nM h⁻¹)</th>
<th>15% APA* (nM h⁻¹)</th>
<th>% of total DIP uptake</th>
<th>% of total APA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bulk plankton</td>
<td>4.8 ± 4.2</td>
<td>0.65 ± 0.74</td>
<td>0.10</td>
<td>99.9</td>
</tr>
<tr>
<td><em>Trichodesmium</em> spp.</td>
<td>0.0067 ± 0.0042</td>
<td>0.076 ± 0.028</td>
<td>0.011</td>
<td>0.1</td>
</tr>
</tbody>
</table>

*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 Kₘ value of about 0.4 μM for both P replete and P deficient 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 PO₄³⁻ 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 PO₄³⁻ uptake values reported in the text (used to calculate the doubling time) differ by 3 orders of magnitude from the graph of PO₄³⁻ 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 Kₘ 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 heterocystous cyanobacteria *Nodularia spumigena* and *Aphanizomenon* sp. occur (Naush et al. 2004). In this area, when P limitation occurred in mid-summer, 91% of PO₄³⁻ 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 (Naush 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 PO₄³⁻ 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 PO₄³⁻ uptake by *Trichodesmium* spp. in the South Pacific, near New Caledonia (Moutin et al. 2005). From P-specific PO₄³⁻ uptake data, the authors calculated that *Trichodesmium* spp. could achieve a growth rate of 0.1 d⁻¹ at a PO₄³⁻ 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), PO₄³⁻ 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 1⁻¹ (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 PO₄³⁻ uptake or APA of *Trichodesmium* spp. by the sum of *Trichodesmium* spp. and bulk seawater PO₄³⁻ 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 PO₄³⁻ 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 (Kₛ) calculated for the picoplankton are about equal to the PO₄³⁻ concentrations found at those same stations: 0.02 μM PO₄³⁻ versus a Kₛ of 0.015 μM at Stn B, 0.01 μM PO₄³⁻ versus a Kₛ 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 Kₛ of 0.78 μM, much greater than the average PO₄³⁻ concentration of 0.04 μM observed during our cruise (March 2004). Based on this data and the average Vₘₐₓ, *Tricho-
**Trichodesmium** 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\(_4^4\) 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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**LITERATURE CITED**


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