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The tropical diazotrophic phytoplankter *Trichodesmium*: biological characteristics of two common species

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ABSTRACT: The 2 tropical cyanobacterial species *Trichodesmium thiebautii* and *T. erythraeum* had similar photosynthetic characteristics in the southwestern Sargasso Sea and Caribbean Sea, with mean rates of light saturated photosynthesis (using O_2 electrode) of 42 (SD = 21.3) and 37 (SD = 18.4) mg O_2 mg chl a^{-1} h^{-1} at 1410 µE m^{-2} s^{-1}, respectively over a 1300 n mile cruise track. Rates of dark respiration were high, and the compensation point for both species was 150 µE m^{-2} s^{-1} (ca 55 m, midday). Estimates of carbon doubling times (using photosynthetic quotient) were from 3.0 to 3.8 d based on expected photosynthetic rates in the water column. The mean rate of nitrogenase activity at 300 µE m^{-2} s^{-1} by *T. thiebautii* averaged 0.45 nmol ethylene colony^{-1} h^{-1}, 1.6 times that of *T. erythraeum* ($p < 0.01$) as observed from samples collected on 3 cruises (64 paired observations). Furthermore, in a comparison of nitrogenase activities, at light intensities between ca 500 and 2500 µE m^{-2} s^{-1}, *T. thiebautii* was about twice as active as *T. erythraeum*. The phycoerythrin content of *T. erythraeum* averaged 260 ng colony^{-1}, 4.4 times that of *T. thiebautii*, and the mean PE : chl *a* ratios were 3.2 and 1.2, respectively. Other pigments: (β-carotene, zeaxanthin, myxoxanthophyll, echinenone, and trace pigments) were similar between the 2 species. The organization of subcellular inclusions was distinctly different in these 2 species. The high abundance of *T. thiebautii* relative to *T. erythraeum* in many tropical seas may be due to higher rates of N_2 fixation and a previously reported neurotoxin in the former species.

INTRODUCTION

Species in the genus *Trichodesmium* Ehrenberg are common phytoplankters in tropical waters, often forming extensive blooms, and are important as primary producers and as a source of new nitrogen via N_2 fixation (Carpenter & Romans 1991). The taxonomic validity of the genus *Trichodesmium* has been noted by Anagnostides & Komarek (1988), and according to Sournia (1968), the genus *Trichodesmium* has 4 marine species: *T. thiebautii* Gomont ex Gomont, *T. erythraeum* Ehrenberg ex Gomont, *T. hildebrantii* Gomont, and *T. contorta* Wille in Schutt. The 2 species which appear to be most common in tropical seas are *T. erythraeum* and *T. thiebautii*, and the intent of this paper is to determine how these 2 species differ in regard to photosynthetic pigments, nitrogenase activity and the response of photosynthesis to irradiance. Recently, a fragment of the *nifH* gene was examined in isolates of these 2 putative species (Ben-Porath, Carpenter & Zehr unpubl.). There were 6 nucleotide differences between them in this highly conserved gene, thus suggesting they are genetically distinct.

These 2 species may be visually distinguished by several criteria. For example, *Trichodesmium thiebautii* colonies are typically made up of trichomes arranged in parallel in a slightly twisted cylindrical pattern much like a piece of rope (Fig. 1). This species usually appears golden-yellow, although color may vary from gray to red. In contrast, *T. erythraeum* colonies are typically flat, in a 'raft' shape, and are usually darker, sometimes dark red, as compared with *T.*

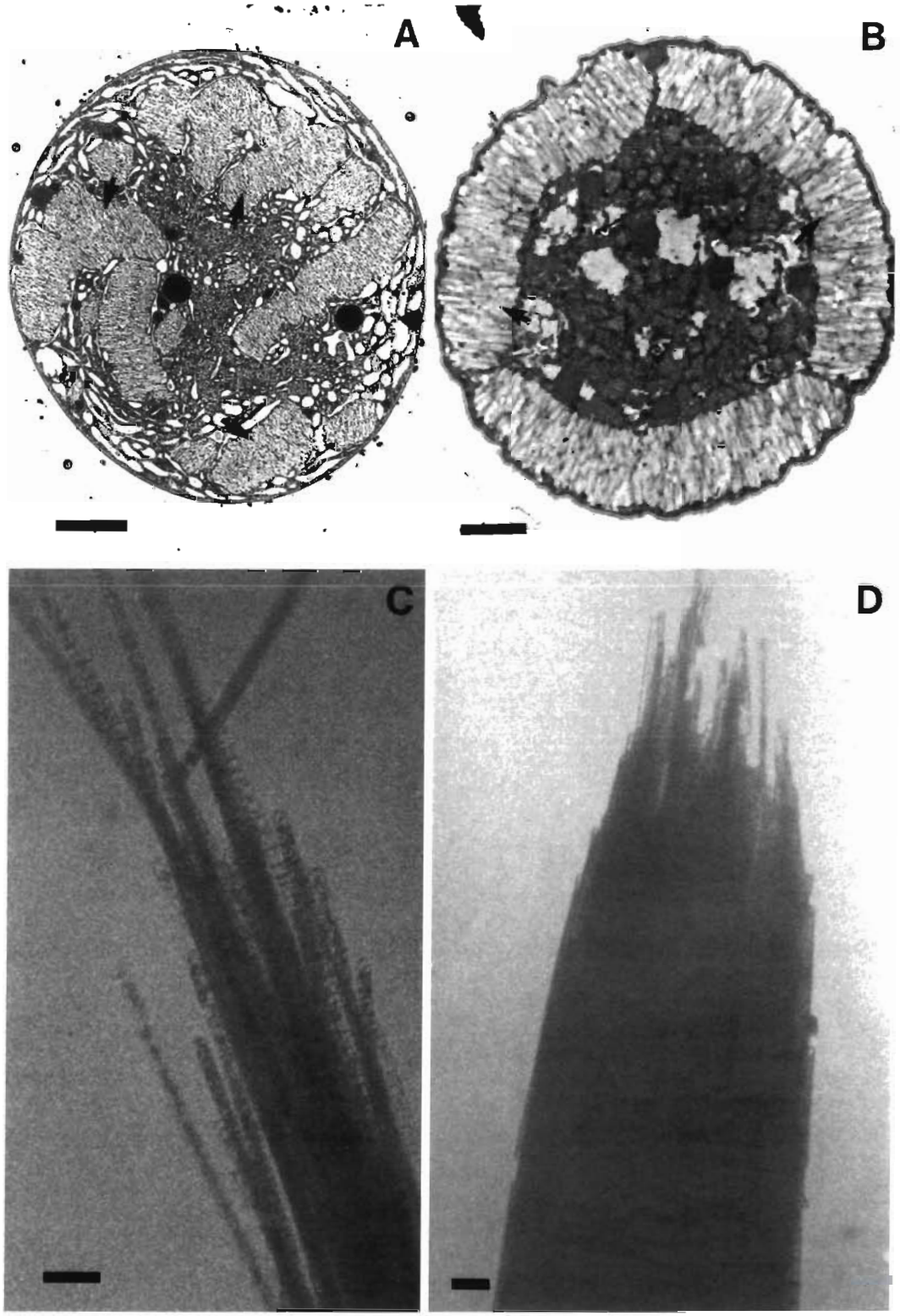

Fig. 1 *Trichodesmium thiebautii* and *T. erythraeum*. Upper: transmission electron micrographs of cross-sections of cells of: (A) *T. thiebautii* (bar = 2 µm), (B) *T. erythraeum* (bar = 1 µm) (arrows indicate gas vesicles). Lower: photomicrographs of (C) *T. thiebautii* and (D) *T. erythraeum* (bar = 5 µm) showing different arrangements of trichomes in colony

thiebautii. If these colonies are in a glass beaker, one observes that *T. erythraeum* colonies are more buoyant than *T. thiebautii* and typically rise to the surface then drift to the sides where they can be easily isolated. Further differences, at the microscopic level, are that *T. erythraeum* cells are either as wide as or wider than long (from 7 to 11 µm wide, rarely to 21 µm), are slightly constricted at the crosswalls and have a cap or a calyptra at the end of the trichome (Desikachary 1959). Cells of *T. thiebautii* are either as long as or up to twice as long as wide (from 7 to 16 µm wide), are not constricted at the crosswalls and have no terminal cap (Desikachary 1959). The collapse pressures of their gas vesicles differ, the mean being 12 bar for *T. erythraeum* and 37 bar for *T. thiebautii* (Walsby 1978). In addition to the collapse pressure differences, Gantt et al. (1984), using transmission electron microscopy, found that the gas vesicles in *T. thiebautii* were smaller and more randomly distributed through the cell than those in *T. erythraeum*. Gas vesicles in *T. erythraeum* are distributed at the outside of the cell, usually in 4 clusters (Fig. 1). Further differences are that polyphosphate bodies appear to be absent in *T. thiebautii*, but have been observed in *T. erythraeum*. However, poly-β-hydroxybutyric acid granules, which are used for carbon and energy storage, are present in *T. thiebautii*, but not in *T. erythraeum* (Siddiqui et al. 1992a, c).

Both species typically coexist in the North Atlantic Ocean, but *Trichodesmium thiebautii* is often the more abundant (Carpenter & Price 1977), and in Sagami Bay along the south coast of Japan, *T. thiebautii* is usually present at a concentration 10 times higher than that of *T. erythraeum*. (Marumo & Nagasawa 1976). However, in some locations such as the Indian Ocean, reports indicate that *T. erythraeum* is often more abundant than *T. thiebautii* (Qasim 1972, Devassy et al. 1978, Bryceson & Fay 1981).

There appear to be no comparative studies on differences in the physiological ecology of these 2 species. To determine how they differ physiologically, we measured pigment content, photosynthesis, acetylene reduction (nitrogenase) activity and microscopy on samples collected on 4 research cruises to the Caribbean Sea on the RV 'Columbus Iselin', and report the results herein.

MATERIALS AND METHODS

Samples were collected from 3 to 24 January and 9 to 20 April 1990, 25 January to 16 February 1991, and 17 January to 6 February 1992 in the Bahama Islands and eastern Caribbean Sea. Collections were made by towing a 1 m diameter net of 222 µm mesh at 15 m depth. Colonies were then isolated with a plastic loop into glass fiber (GF/F) filtered seawater and rinsed again. For transmission electron microscopy, colonies were fixed, dehydrated, and embedded in epoxy resin as described previously (Siddiqui et al. 1992b). Thin sections were observed on a Zeiss 10 TEM at 60 kV. For measurement of acetylene reduction, we followed the basic procedure outlined by Capone et al. (1990) for the January 1990 measurements. In these studies, 15 colonies of either *Trichodesmium erythraeum* or *T. thiebautii* were placed in 5 ml of filtered seawater in a 9 ml glass serum bottle. Samples were incubated indoors in a flowing (taken from 1 m depth) seawater bath with exposure to light (300 µE m^{-2} s^{-1}) from a Sylvania or a Colorspec 500 W incandescent lamp. For a comparison of nitrogenase activity at ambient light, colonies were collected on 19 April 1990, prepared in serum bottles as described above, and incubated in a flowing seawater incubator in full sunlight (ca 2500 µE m^{-2} s^{-1}). Ethylene was measured on 100 µl samples of the gas phase which were injected into a Shimadzu Mini II gas chromatograph.

Photosynthesis was determined by measuring oxygen production or consumption with a Hansatech CB1-D electrode control box, and DW1 electrode unit and reaction vessel. Typically, 5 colonies were placed in 1 ml of glass fiber (GF/F) filtered seawater in the reaction vessel, and were cradled above the teflon-covered stir bar on a piece of 64 µm mesh netting which was held in place with a ring of polyethylene plastic. The netting ring allowed the colonies to remain intact, prevented contact with the stir bar, yet allowed complete circulation of water in the reaction chamber Temperature around the reaction vessel in the plexiglass water jacket was controlled by water from a circulating water bath (Forma 2095). This was set at ambient water temperature (26.5 to 28.0 °C).

For the photosynthesis (P) vs irradiance (I) curves, the light source was a Vivitar 3000AF 35 mm slide projector with an Osram HLX Xenophot bulb. Light intensities, measured with a Biospherical Inst. Co. QSP-170 Scalar Irradiance meter, were: dark, 10, 20, 50, 105, 315, 630, 1410, and 1950 µE m^{-2} s^{-1} and were used in that order (ascending from darkness to highest intensity). Neutral density slides were made with layers of shading film (Cello-Tek Mfg. Co.) set in 35 mm slide holders. Change in oxygen concentration was measured at each light intensity for from 2 to 4 min. Moles oxygen evolved was converted to moles carbon fixed using a photosynthetic quotient (PQ) of 1.25. After a P vs I curve was run, the chlorophyll *a* content of the colonies was determined by filtering the entire sample onto a 25 mm diameter GF/C filter, then placing the filter in 6 ml of 100% methanol and keeping it in a freezer overnight. The chlorophyll in the extracted sample was then determined, as recommended by

Holm-Hansen & Reimann (1978), by fluorescence with a Turner 111 fluorometer. To calculate P vs I curves and the parameters P_{max}, α, and I_k, oxygen production data were fitted to curves using the formula given by Smith (1936) as follows:

$$P = P_{max} \frac{I/I_k}{[1 + (I/I_k)^2]^{1/2}} + R$$

where I = irradiance; I_k = light intensity at the junction of the initial slope and P_{max}; and R = rate of dark respiration. The respiration term (R) was added to Smith's equation to yield net photosynthesis.

Pigment content of the 2 species was determined using a high performance liquid chromatography (HPLC) system for the chlorophyll and carotenoid components in January and February 1991. From 5 to 20 colonies of *Trichodesmium thiebautii* or *T. erythraeum* were picked fresh from tows, and extracted immediately by sonication with 100% acetone followed by overnight extraction in the freezer. After centrifugation, the extract was injected into a reverse-phase HPLC, and pigments were separated at a flow rate of 1.1 ml min^{-1} with a gradient of 90% acetonitrile/water which was increased to 100% ethyl acetate over 35 min. The equipment used consisted of a Shimadzu pump with an ELAB low pressure mixing controller programmed by an IBM AT computer, with detection at 436 nm (Waters 440 detector). A fixed loop (250 µl) electrically actuated Valco injector delivered sample extracts to the analytical column (Alltech Adsorbosphere C-18, 25 cm × 4.6 mm, 5 µm). The instrument was calibrated with authentic standards previously measured in the home laboratory and stored frozen on board ship. These included chlorophyll *a*, zeaxanthin, and β-carotene. Myxoxanthophyll concentrations were quantified using an extinction coefficient of 2160 $E^{1\%}_{cm}$ in the absence of a pure standard. In April 1990, chlorophyll *a* was also measured using a Turner 111 fluorometer as described previously (McCarthy & Carpenter 1979). The phycoerythrin (PE) content was measured using a Turner Designs fluorometer and the glycerol-uncoupling procedure of Wyman (1992). The fluorometer was calibrated using a water extract of natural *Trichodesmium* and the extinction coefficients of Moreth & Yentsch (1970).

RESULTS

Pigments. The phycoerythrin content of *Trichodesmium erythraeum* averaged approximately 4.4 times that of *T. thiebautii*. On 6 and 14 January 1990, mean PE content of *T. erythraeum* was 260 (SD = 51) ng $colony^{-1}$, and the mean for *T. thiebautii* was only 61 (SD = 49) ng PE $colony^{-1}$ (Table 1). The mean chlorophyll *a* contents of *T. erythraeum* and *T. thiebautii* were similar, 69.1 (SD = 49) and 47.6 (SD = 20) ng $colony^{-1}$, respectively, but the variance was high. We observed mean PE:chl *a* ratios of 3.7 for *T. erythraeum* and 1.3 for *T. thiebautii*. In surface water samples collected in 1973 and 1974 south of Japan, the PE content (weight) of *T. erythraeum* averaged 4.4 and 5.2 times that of the chl *a* in *T. thiebautii* (Aruga et al. 1975). In our measurements, the numbers of trichomes per colony were virtually identical in the 2 species (Table 1), so differences in PE content were not simply due to the presence of more trichomes in a colony.

The dominant pigments, other than phycoerythrin, were chl *a*, β-carotene, zeaxanthin and myxoxanthophyll (Table 2). Echinenone was also present in varying proportions. This pattern of pigments agrees with previous reports (Hogetsu & Watanabe 1975) with the exception that these workers did not report presence of zeaxanthin. A typical chromatogram (Fig. 2) showed trace quantities of *cis* isomers of zeaxanthin, chl *a* allomer and epimer, *cis*-echinenone and an unknown pigment. The unknown component (Fig. 2) had a very similar retention time to that of an acyclic carotene. In general, the samples from the February 1991 cruise showed little signs of appreciable chlorophyll degradation and no phaeophorbides or phaeophytin were detected.

Photosynthesis. Measurements indicated that *Trichodesmium eryth-*

Table 1. *Trichodesmium erythraeum* and *T. thiebautii*. Chlorophyll *a* content (ng $colony^{-1}$), phycoerythrin (PE) (ng $colony^{-1}$) and trichomes per colony collected in the northeastern Caribbean Sea from 15 m depth on 6 and 14 January 1990. Data are from several colonies for each measurement. –: not measured

Date	*T. erythraeum*			*T. thiebautii*		
	Chl *a*	PE	Trichomes	Chl *a*	PE	Trichomes
6 Jan	68	269	406	48	58	465
	119	320	467	51	48	505
	168	172	490	51	98	441
14 Jan	33	239	640	17	33	287
	17	294	320	89	70	498
	34	–	–	33	–	–
	82	–	–	34	–	–
	32	–	–	58	–	–
Mean	69	259	465	48	61	439
SD	49	51	106	20	22	79

Table 2. *Trichodesmium erythraeum* and *T. thiebautii*. Pigment content. Samples were collected between 5 and 20 m depth, water temperature of 26 °C, from 6 to 9 February 1991 in the northeastern Caribbean Sea. Data are ng colony^{-1} for duplicate samples. nd: not detectable

Pigments	*T. erythraeum*	*T. thiebautii*
Chl *a*	37.2	26.7
	16.6	48.8
β-carotene	0.9	0.6
	nd	6.8
Zeaxanthin	1.8	2.9
	2.9	4.8
Myxoxanthophyll	nd	0.9
	0.3	0.4

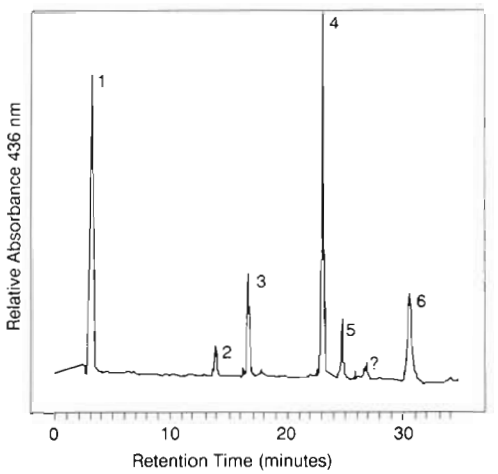

Fig. 2. *Trichodesmium thiebautii*. Reversed phase chromatogram of an acetone extract of a single tuft from 5 m depth, February 1991. Peak identities: 1, solvent front; 2, myxoxanthophyll; 3, zeaxanthin; 4, chlorophyll *a*; 5, echineone; 6, β-carotene

raeum and *T. thiebautii* were very similar in their photosynthetic characteristics. Eight *P* vs *I* curves were collected for *T. erythraeum*, and 22 for *T. thiebautii* in the daytime (between 09:30 and 18:30 h) in a 15 d period in February 1992 (Fig. 3) over a cruise track which spanned 1300 n miles. Fewer data points were collected for *T. erythraeum* because this species was not as abundant as *T. thiebautii*. Although mean photosynthetic rates for *T. thiebautii* were consistently higher than those from *T. erythraeum*, standard errors for the rate measured at each irradiance overlapped, and there was no statistical difference between the 2 curves (Fig. 3). At 1410 μE m^{-2} s^{-1}, mean rate of O_2 production for *T. thiebautii* was 45 mg O_2 mg chl a^{-1} h^{-1}, and for *T. erythraeum* the rate averaged 39. At the high light value of 1950 μE m^{-2} s^{-1}, a small (ca 15%) amount of photoinhibition may have been evident for *T. erythraeum*; however, O_2 production of colonies was only measured for 2 min at each light intensity, and photoinhibition may be more severe when held longer. Mean rates of C fixation (calculated using a PQ of 1.25) at 1410 μE m^{-2} s^{-1} were 13.6 and 11.7 mg C mg chl a^{-1} h^{-1} for *T. thiebautii* and *T. erythraeum*, respectively. The mean light compensation point ($P = R$) for each was the same, 150 μE m^{-2} s^{-1}. The calculated average P_{max} for *T. thiebautii* was 42 (SD = 21.3) mg O_2 mg chl a^{-1} h^{-1}, and for *T. erythraeum* it was 37 (SD = 18.4) (Table 3). The mean respiration rate of *T. erythraeum* averaged 67% higher, −24.9 mg O_2 mg chl a^{-1} h^{-1}, than the mean of −14.9 observed for *T. thiebautii* (Table 3). Furthermore, *T. thiebautii* saturated at a higher light intensity than *T. erythraeum*, and the I_k values were 687 and 324 μE m^{-2} s^{-1}, respectively. Mean dark respiration rates in both species were positively correlated with P_{max} (Fig. 4). A linear regression indicated an *R* value of 0.63. Slopes for the 2 species were virtually identical, so data were pooled for one regression ($Y = 6.38 + 0.24$). An analysis of respiration and P_{max} during day-

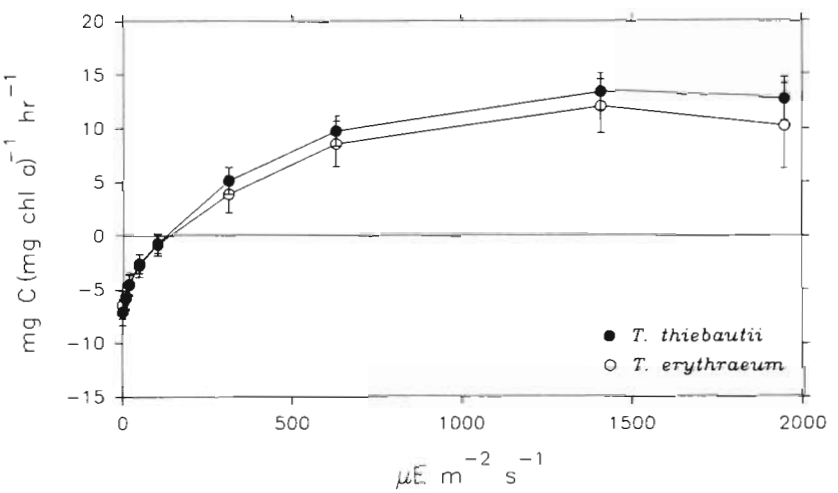

Fig. 3. *Trichodesmium thiebautii* and *T. erythraeum*. Photosynthesis (*P*) vs irradiance (*I*) curves obtained from O_2 electrode and converted to carbon using a PQ of 1.25, in January and February 1992 in Bahamas and northeastern Caribbean Sea. The *T. thiebautii* curve shows means and SEs (bars) of 24 profiles taken between 08:45 and 17:00 h. The *T. erythraeum* curve is the mean of 8 profiles

Table 3. *Trichodesmium erythraeum* and *T. thiebautii*. Means and SDs of photosynthetic parameters. *T. erythraeum*: n = 8; *T. thiebautii*: n = 21

	T. erythraeum		*T. thiebautii*	
	Mean	SD	Mean	SD
P_{max}[a]	36.9	18.4	41.9	21.3
Resp.[a]	−24.9	5.16	−14.9	6.10
α	0.108	0.068	0.067	0.023
I_k[b]	324.2	215.5	686.5	754.5

[a] mg O_2 mg chl a^{-1} h^{-1}; [b] μE m^{-2} s^{-1}

light indicated no relationship between time of sampling and either of these parameters (data not shown).

Nitrogenase activity. For 64 paired comparisons, collected on 3 cruises, of acetylene reduction at 300 μE m^{-2} s^{-1}, *Trichodesmium thiebautii* averaged 0.45 and *T. erythraeum* averaged 0.28 nmol ethylene produced colony^{-1} h^{-1} (Fig. 5). A paired *t*-test of the means gave significant differences ($p < 0.01$). A comparison of the species on 19 April 1990 indicated that *T. thiebautii* nitrogenase activity was about twice as active as *T. erythraeum* at saturating light intensities (Fig. 6). *T. thiebautii* may have had some inhibition in nitrogenase activity at full surface light intensity, whereas *T. erythraeum* showed progressive increases up to full surface light intensity.

Particulate C and N content. Carbon and nitrogen contents of colonies were virtually identical on the one date they were compared, 7 February 1991. *Trichodesmium thiebautii* had 11.9 μg C and 2.32 μg N, while *T. erythraeum* averaged 11.2 μg C and 2.18 μg N (Table 4). The C : N ratios were 5.13 for *T. thiebautii* and 5.15 for *T. erythraeum*.

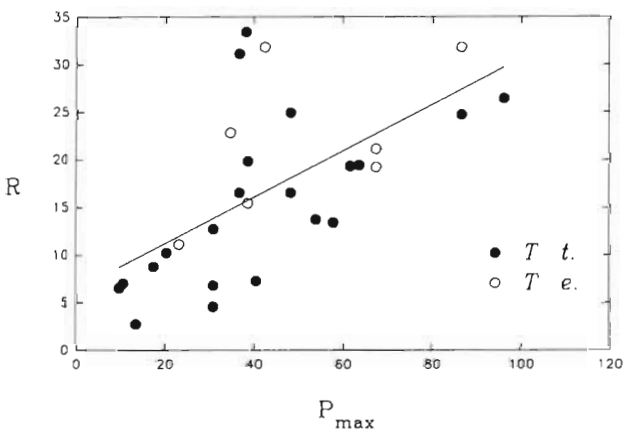

Fig. 4. *Trichodesmium thiebautii* (○) and *T. erythraeum* (●). Scatter plot of dark respiration (R) in mg O_2 mg chl a^{-1} h^{-1} and P_{max} (same units). P_{max} was estimated using model of Smith (1936)

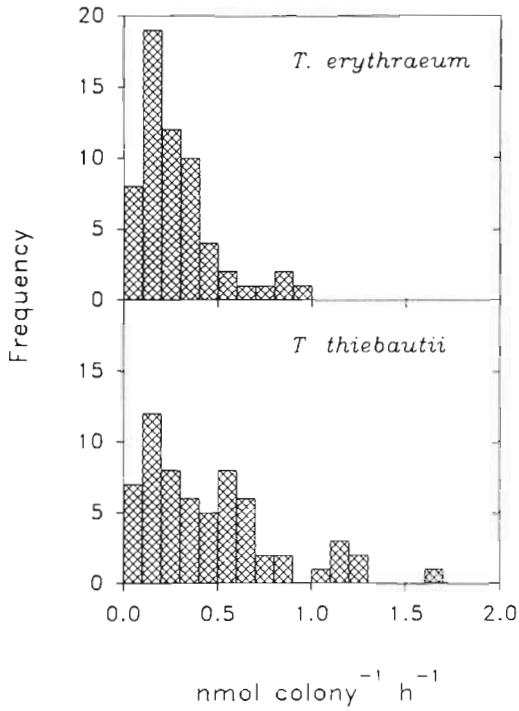

Fig. 5. *Trichodesmium thiebautii* and *T. erythraeum*. Histograms of acetylene reduction in nmol ethylene produced colony^{-1} h^{-1}

DISCUSSION

There were distinct differences between the 2 species examined. *Trichodesmium thiebautii* had greater nitrogenase activity at irradiance values found in tropical near-surface waters, and it also had the advantage of possessing a neurotoxin which inhibits grazing by some copepods (Hawser & Codd 1992). However, *T. erythraeum* is more buoyant, and has higher concentrations of phycoerythrin. There are other ultrastructural differences, but both are similar as regards photosynthetic rates and photosynthetic pigments other than phycoerythrin.

Overall, both species are clearly adapted to and in need of high light intensities relative to most other marine phytoplankters. The mean I_k values, water column irradiances above which light-saturated photosynthesis occurs, were 324 and 686 μE m^{-2} s^{-1} for *Trichodesmium erythraeum* and *T. thiebautii*, respectively (Table 3). These irradiances were similar to that reported by Li et al. (1980) who calculated an I_k of 358 μE m^{-2} s^{-1} for *T. thiebautii*. Using the observed extinction coefficients (Subramaniam & Carpenter unpubl.) collected with a Biospherical Inst. Co. spectroradiometer on the January 1991 cruise, the typical depths at which these values would be found during midday are at approximately 23 and 35 m. Thus for

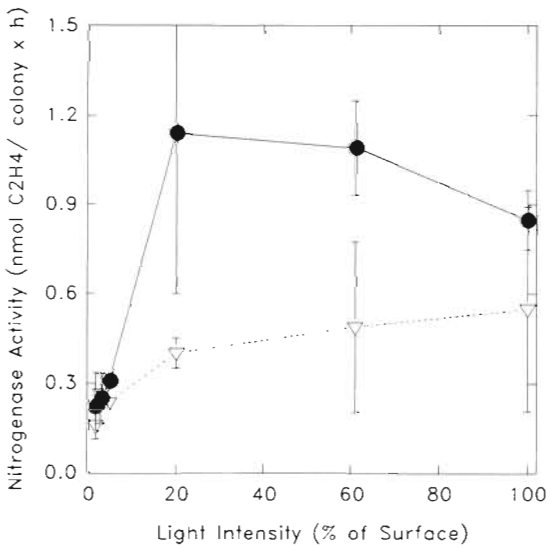

Fig. 6. *Trichodesmium thiebautii* (▽) and *T. erythraeum* (●). Nitrogenase activity at different light intensities. Bars show SD

these species, light-saturated photosynthesis occurs within the region where their population maxima (15 m, Caribbean Sea and southwestern Sargasso Sea; Carpenter & Price 1977) typically are found.

Walsby (1978) has noted the more rapid floating velocity in *Trichodesmium erythraeum* as compared with *T. thiebautii*. He speculated that this buoyancy may prevent it from being mixed as deeply as *T. thiebautii*, since *T. erythraeum* has weaker gas vesicles. Those in *T. erythraeum* would collapse at 120 m, while *T. thiebautii* could sink to 370 m before rupture. This being so, we might thus expect that *T. erythraeum* should therefore be restricted to depths closer to the surface than *T. thiebautii*.

Both species have high rates of respiration, as evidenced here, and previously by Kana (1992). The mean compensation light intensity of 150 μE m^{-2} s^{-1} (Fig. 2) is the 6 % light level (I_o = 2500 μE m^{-2} s^{-1}) and this would occur at about 55 m depth (Subramaniam & Carpenter unpubl.). Carpenter & Price (1977) had observed earlier that virtually the whole *Trichodesmium* population in the Caribbean Sea occurs within the upper 50 m, well above the compensation light intensity. Kana (1992), working in the same region, measured an even higher light compensation point of 280 μE m^{-2} s^{-1} for *Trichodesmium*.

Table 4. *Trichodesmium erythraeum* and *T. thiebautii*. Particulate C and N content colony^{-1} on 7 February 1991 in the northeastern Caribbean Sea. From 12 to 25 colonies were used for each measurement

Species	μg C	μg N	C:N
T. thiebautii	12.1	2.29	5.26
	11.7	2.34	5.00
T. erythraeum	11.3	2.20	5.14
	11.1	2.15	5.16

Two striking characteristics of the data are the high variation in respiration and P_{max} and their positive correlation (Fig. 4). Our data indicate about a 10- and a 4-fold range in dark respiration values for *Trichodesmium thiebautii* and *T. erythraeum*, respectively, with a positive correlation with P_{max} for both species (Fig. 4). The causes of this high variation in respiration and P_{max} are unknown. Previous research on nitrogenase activity indicates very high (100-fold) variation in activity among colonies collected and assayed simultaneously (Carpenter unpubl.). Colonies at any one depth differ in regard to buoyancy characteristics and presumably to past light history, and this may result in high variation in photosynthetic characteristics. Colony-associated bacteria, protozoa and other heterotrophs certainly contribute to oxygen consumption, but not to evolution, so they could not possibly be a cause of the observed correlation (Fig. 4). Secondly, the cyanobacteria were collected in daytime and were actively photosynthesizing in the water column when collected at 15 m, thus the dark respiration rate must partially reflect their metabolic activity prior to collection. Those with high rates of photosynthesis likely had a high ATP requirement when placed in the dark, and oxidative phosphorylation, using carbohydrate reserves, must also have been high. The fact that N_2 fixation in this species is closely coupled to photosythesis may play a role in the observed correlation between respiration and P_{max}. Recently a positive correlation between cytochrome oxidase activity and nitrogenase has been observed in *Trichodesmium* (Bergman, Siddiqui, Carpenter & Peschek unpubl.), thus suggesting a linkage of these 2 processes.

Maximal rates of photosynthesis appear to be slightly greater for *Trichodesmium thiebautii* than for *T. erythraeum*, and respiration rates were higher in the latter species. If *T. erythraeum* is slightly less efficient at photosynthesis, then perhaps its more buoyant nature and exposure to higher light intensities would compensate for its lower photosynthetic efficiency. A further point is that every one of the rather limited number of colonies of *T. erythraeum* collected by Walsby (1978) was positively buoyant, whereas a significant percentage of *T. thiebautii* observed by him were not. In fact, Villareal & Carpenter (1990) noted diel changes in buoyancy in *T. thiebautii*, but not enough *T. erythraeum* were collected to make conclusions regarding changes in this species. We observed the highest mean rates of photosynthesis at 1410 μE

m^{-2} s^{-1}, and it averaged 13.6 (SD = 6.17) and 11.6 (SD = 5.52) mg C mg chl a^{-1} h^{-1} for *T. thiebautii* and *T. erythraeum*, respectively. This is considerably higher than the rates measured by Hogetsu & Watanabe (1975) southeast of Japan. They observed P_{max} values from 1.09 to 3.44 (av. = 1.72) mg C mg chl a^{-1} h^{-1} at 22 to 23 °C, and lower values were seen at 21 °C in January. Field measurements of P_{max} made on samples collected by Lewis et al. (1988) during a bloom in the Sargasso Sea at 28°C indicated a maximal rate of photosynthesis of 3.78 mg C mg chl a^{-1} h^{-1} for *Trichodesmium*. Strong photoinhibition was observed by Lewis et al. (1988) at irradiances above about 1000 µE m^{-1} s^{-1}. It may well be that photoprotectant pigments vary with the physiological state of the population, and this may explain why photoinhibition is seen in some natural samples, but not in others. Furthermore, Lewis et al. (1988) used longer ^{14}C incubations to measure photosynthesis, and exposure to high light for long periods may have led to photoinhibition.

The calculated rates of carbon fixation in our study were high and indicate that the population in the southwestern North Atlantic was growing rapidly. Cellular carbon doubling times can be calculated for the populations in near-surface waters. With midday photosynthetically active radiation (PAR) values of 2500 µE m^{-2} s^{-1} at the sea surface, and the 50% light level at 15 m, the depth of population maxima, the bulk of the *Trichodesmium* population should be photosynthesizing optimally. The total carbon fixed at 1410 µE m^{-2} s^{-1} in 10 h of daylight for a colony which contained 50 ng chl *a* (Carpenter 1983) was 5.9 µg C for *T. erythraeum* and 6.8 µg C for *T. thiebautii*. The rate of respiration of colonies is lower at night than during the day (T. Roenneberg & E. J. Carpenter unpubl.), and data collected between sundown and sunrise on the same cruise gave a mean (21 measurements) respiration rate of 4.1 µg C µg chl a^{-1} h^{-1}. The 14 h of respiration per night yielded a total night time respiration of 2.9 µg C $colony^{-1}$. Applying this rate to both species, results in a total net carbon fixation rate of 3.9 and 3.0 µg C $colony^{-1}$ d^{-1} for *T. thiebautii* and *T. erythraeum*, respectively. Particulate carbon content of these colonies averaged 11.2 µg C for *T. erythraeum* and 11.9 µg C for *T. thiebautii* (Table 4). Using these mean particulate carbon values, the carbon doubling times at 1410 µE m^{-2} s^{-1} would be 3.0 (SD = 1.56) d for *T. thiebautii* and 3.8 (SD = 1.82) d for *T. erythraeum*. These values should be typical of division rates in the euphotic zone at light intensities above I_k (Table 3), and are considerably faster than that of 18 d determined by Li et al. (1980) in the southeastern Caribbean Sea, but similar to doubling times based on nitrogen recently calculated by Carpenter et al. (1987). Furthermore, these carbon doubling times are about 3 times faster than the average of 10 d used by Carpenter & Romans (1991) in estimating the importance of *Trichodesmium* in the tropical North Atlantic Ocean. Considering that the mean of 3.0 and 3.8 d occurred over a 1300 n mile transect, and is about 3 times more rapid than the doubling time used by Carpenter & Romans (1991), it is probable that *Trichodesmium* may be more important in oceanic C and N cycling than calculated.

Both species have relatively high concentrations of the accessory pigment phycoerythrin (PE). The PE in *Trichodesmium* absorbs over a relatively broad wavelength, having 3 peaks (Fujita & Shimura 1975), and is efficient in the transfer of light energy to chl *a*. Because of this, the calculation of photosynthetic rates based on chl *a* can be misleading, giving the appearance that *Trichodesmium* spp. are more active in regard to photosynthetic capacity than phytoplankton which have no PE.

Paradoxically, the observed 4-fold higher concentrations of (PE) in *Trichodesmium erythraeum*, as compared with *T. thiebautii*, would appear to be characteristic of a deep-water species accustomed to living at low light intensities rather than that of a more highly buoyant species. The reason for the higher PE content in *T. erythraeum* is thus far unknown, but it may be related to the fact that the nitrogen storage reserve, cyanophycin, has been observed in *T. thiebautii* but not in *T. erythraeum* (Siddiqui et al. 1992c). Phycoerythrin may function as a nitrogen storage reserve in *T. erythraeum*.

Differences in content of other pigments in these 2 species were not immediately obvious. Previous research by Hogetsu & Watanabe (1975) has indicated the presence of β-carotene, echinenone and myxoxanthophyll in addition to PE and chl *a* (Hogetsu & Watanabe 1975). They also found a very high degree of variability in pigment content from one location to another. During 3 research cruises over 3 yr between 1971 and 1973, the β-carotene content, as a percentage of chl *a* (weight), ranged from 1 to 23% and averaged 8.8%. The mean echinenone content was less than 0.1% of the chl *a*, while myxoxanthophyll averaged 1.7%, and reached as much as 11% of the chl *a*.

The reasons for the dominance of *Trichodesmium thiebautii* or *T. erythraeum* in some locations are not immediately clear, since photosynthetic characteristics of the 2 species were very similar, and growth rates were not greatly different. Acetylene reduction rates of *T. thiebautii* averaged 1.6 times greater than *T. erythraeum* on a per colony basis, suggesting better capacity for N_2 fixation. One major factor regulating abundance of these species might be the presence of a neurotoxin (Hawser et al. 1991) which has been observed in *T. thiebautii*, but not in *T. erythraeum*, and this may allow more grazing to occur on the latter spe-

cies. There are further possible differences in ultrastructure which may affect abundance, for example, cyanophycin granules (N storage), vacuole-like structures, and scroll bodies have not yet been observed in *T. erythraeum*, whereas they have in *T. thiebautii* (Siddiqui et al. 1992c). The absence of these ultrastructures may affect the survival ability of *T. erythraeum*.

In conclusion, 2 planktonic cyanobacteria, *Trichodesmium thiebautii* and *T. erythraeum*, are similar as regards particulate C and N content, and photosynthetic rates. They differ in that *T. erythraeum* has a higher phycoerythrin content, but a lower rate of nitrogenase activity at saturating light intensities. Previous studies have shown differences in some cell inclusions, as well as in buoyancy and gas vesicle collapse pressure. Both appear to be well adapted to photosynthesis at high light intensities in near surface waters, and our measurements indicate very high photosynthetic capacity and the potential for high growth rates at light intensities typically found at their depth maxima. Particulate carbon turnover times indicate that, at the light intensities found at its depth maxima (15 m), these species are dividing at a relatively rapid and consistent rate over a large region of the southwestern North Atlantic Ocean.

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