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Photosynthetic characteristics of *Trichodesmium* in the southwest Pacific Ocean: importance and significance

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ABSTRACT: The photosynthetic capacities of *Trichodesmium* were investigated in a multidisciplinary study comprising 9 cruises in a region of the Coral Sea, southwest Pacific Ocean, where these diazotrophic cyanobacteria are particularly abundant. Thirty specific measurements of photosynthesis in natural communities of *Trichodesmium* using an O_2 electrode with the addition of a ^{14}C-tracer gave a mean photosynthetic quotient of 1.19, quite close to the theoretical value. Seven photosynthesis vs. irradiance curves exhibited typically high light-saturated and compensation photosynthetic parameters I_k and I_c (327 and 77 µE m^{-2} s^{-1}, respectively), implying that *Trichodesmium* requires a stronger irradiance for growth than other phytoplankton typical of oligotrophic systems. The vertical profiles of *in situ* productivity of *Trichodesmium* generally showed a maximum at 10 or 20 m depth and a lower value at the surface, the latter probably being due to photoinhibition. Based on productivity data and the mean measured C:chl *a* ratio of 188 g C g chl a^{-1}, the maximum *Trichodesmium* growth rate ranged between 0.18 and 0.32 d^{-1}. The high level of energy required by these organisms to grow could explain why the vertical distribution of *Trichodesmium* colonies is generally restricted to well-lit surface waters. Furthermore, our observations suggest that the presence of a shallow mixed-layer is a prerequisite for an optimal light regime and a maximum growth rate for this genus. Hence, the seasonal changes in both incident radiation and water column stratification would strongly control the variations in the abundance of *Trichodesmium* populations, which tends to be minimum in winter and spring and maximum in summer.

KEY WORDS: *Trichodesmium* photosynthesis · Primary productivity · Photosynthetic quotient · Cyanobacteria · Marine diazotrophs · Southwest Pacific Ocean

INTRODUCTION

Trichodesmium is a genus of filamentous non-heterocystous cyanobacteria that is considered responsible for the majority of N_2 fixation in the ocean (Capone et al. 2005). The input of biologically available nitrogen to the water column through N_2 fixation tends to increase the net primary production and hence the export of particulate organic carbon (POC) to the deep ocean (Karl et al. 2002). Therefore, the N_2 fixed by *Trichodesmium* would contribute to 2 important processes at the global scale: (1) increase in the biological sequestration of atmospheric CO_2, thus fuelling the biological pump (Eppley & Peterson 1979); (2) compensation for the probable imbalance in the modern ocean nitrogen budget due to N loss by denitrification (Codispoti et al. 2001).

To estimate diazotrophy at the global scale, the main environmental factors that determine the distribution (including bloom formation) and growth of *Trichodesmium* must be explained, especially in areas

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known to be favourable but poorly documented, such as the southwest Pacific Ocean (LaRoche & Breitbarth 2005, Campbell et al. 2005). *Trichodesmium* cells characteristically occur as filaments (trichomes) or colonies (Capone et al. 1997), which at times accumulate massively at the sea surface, producing reddish water, with concentrations up to 10^5 or 10^6 trichomes l^{-1} (Sournia 1968, Revelante & Gilmartin 1982). This organism has most often been reported from regions between 30° N and 30° S in the 3 major oceans (Capone et al. 2005, LaRoche & Breitbarth 2005). In the southwest Pacific (SWP), surface blooms have been observed during naval and aerial surveys (Dupouy et al. 2004). Extensive chlorophyll enrichments detected by the Coastal Zone Color Scanner (CZCS; summer 1982) and Seaviewing Wide Field-of-view Sensor (SeaWiFS; summer 1998) that covered surfaces of up to 90 000 km^2 around New Caledonia were attributed to *Trichodesmium* (Dupouy et al. 1988). Blooms of *Trichodesmium* were also reported in the spring-summer period in the Tonga Islands (Bowman & Lancaster 1965) and in the Great Barrier Reef of Australia, with concentrations of 10 000 trichomes l^{-1} in surface accumulations (Revelante & Gilmartin 1982). Thus, in contrast to many other large oligotrophic areas of the tropical oceans where these organisms are scarce or totally absent, the SWP appears to be remarkably favourable for *Trichodesmium* development. Hence, this region is particularly convenient for an investigation of the main physical, chemical and biological processes that control *Trichodesmium* growth and population dynamics.

Several environmental factors have been suggested to control *Trichodesmium* growth and N_2 fixation, among which are temperature, nutrients such as phosphorus and iron, and light. *Trichodesmium* growth seems to be favoured in warm seas (LaRoche & Breitbarth 2005). In the SWP, all *Trichodesmium* blooms were observed in water in which the temperature exceeded 22°C (Dupouy et al. 2004, Moutin et al. 2005). Furthermore, *Trichodesmium* was shown to be adapted to the low concentrations of available phosphate (Wu et al. 2000). In the SWP, a critical inorganic phosphate concentration as low as 9 nM was required by *Trichodesmium* populations for maintaining a significant positive growth rate (Moutin et al. 2005). The concentrations of phosphate in that region were observed to be higher than 9 nM in winter and spring, but generally lower than 9 nM in summer and autumn (Van den Broeck et al. 2004). Because most *Trichodesmium* blooms occur in summer, precisely in the period when inorganic phosphate tends to fall below this critical level (Moutin et al. 2005), this observation suggests that *Trichodesmium* would have the capacity to utilize other sources of P, such as dissolved organic phosphate (Mulholland et al. 2002).

Considering the aeolian distribution of iron in the ocean and the high iron requirements of *Trichodesmium* (Berman-Frank et al. 2001), nitrogen fixation by this organism would be iron-limited in large parts of the global ocean (Berman-Frank et al. 2001). However, in the SWP, relatively high iron concentrations (200 to 400 pM) were observed at 1 station north of New Caledonia by Nakayama et al. (1995); in contrast, Campbell et al. (2005) reported surface iron concentrations that ranged between less than the analytical detection limit of 60 and 320 pM at 4 stations north of New Caledonia. Without any information on *in situ* iron uptake kinetics, it is difficult to determine when and where the iron needs of *Trichodesmium* are partially or totally satisfied in the SWP.

As a possible consequence of nutrient stress (P, Fe or other), the *Trichodesmium* growth rate has been reported to be very slow (Mague et al. 1977). However, some recent field studies suggest that *Trichodesmium* would have a carbon-doubling time ranging from 3 to 5 d (LaRoche & Breitbarth 2005), which is faster than previously found but significantly slower than the growth rate of most other phytoplankton species estimated in the western equatorial Pacific (Le Bouteiller et al. 2003). Growth rates of *Trichodesmium* have not been documented in the South Pacific. Assuming the same pattern in the Pacific as in the Atlantic, it is now important to gain an understanding of the formation of widespread and intense blooms by a slow-growing organism such as *Trichodesmium*.

With only 1 or 2 cellular divisions per week, the control of *Trichodesmium* photosynthesis and growth by light availability is expected to be preponderant. A number of studies in the Atlantic Ocean (Li et al. 1980, Kana 1993, Carpenter et al. 1993, Roenneberg & Carpenter 1993, Carpenter & Roenneberg 1995, Villareal 1995) demonstrated that *Trichodesmium* spp. are adapted to growing under high levels of irradiance, as shown by a high mean value of the photosynthetic saturation parameter I_k (close to 300 µE m^{-2} s^{-1}). Similarly, the light compensation index (I_c) is much higher in *Trichodesmium* spp. (59 to 280 µE m^{-2} s^{-1}) than in other phytoplankton species (typically <10 µE m^{-2} s^{-1}), and displays highest values at midday and lowest values at night (Kana 1993, Roenneberg & Carpenter 1993).

The purpose of this study was to describe the photosynthetic characteristics of *Trichodesmium* in a region where these properties were still unknown, using results of *in situ*, simulated *in situ* and laboratory experiments. Results were used to define the optimal light regime required for *Trichodesmium* growth and to determine whether this light regime could be one of the constraining environmental factors that accounts for the space-time distribution of *Trichodesmium* in the SWP.

MATERIALS AND METHODS

To obtain a robust evaluation of the photosynthetic characteristics of *Trichodesmium* in the SWP, the photosynthetic capacities of natural populations of *Trichodesmium* were determined in the laboratory and under *in situ* and simulated *in situ* conditions.

Sampling for laboratory and simulated *in situ* experiments. All sampling was conducted at only 1 location, in Saint Marie Bay (SW New Caledonia lagoon) within an operating area of 1 km diameter (Fig. 1). The water column (10 to 15 m depth) of this lagoon area was most often homogeneous. Samples were collected using a 35 µm-mesh plankton net towed very slowly just under the surface for 1 to several minutes, often crossing slicks of *Trichodesmium* on the sea surface. The content of the collector was gently poured into a 10 l polycarbonate bottle maintained in the dark, pending its rapid return to the laboratory (within 20 to 30 min). On most occasions, the predominant species in these samples was *T. erythraeum*.

Measurement of photosynthesis vs. irradiance in the laboratory. Seven experiments were carried out in December 2002, in order to obtain photosynthetic production per unit biomass (*PB*) vs. irradiance (*I*) curves. Sampling was conducted between 07:00 and 12:00 h. *PB* is the amount of O_2 produced or carbon fixed per hour normalized to chlorophyll *a* (chl *a*), expressed in mg O_2 mg chl a^{-1} or mg C mg chl a^{-1} h^{-1}). In the laboratory, freshly collected samples were dispensed into 3 or 4 plastic pails, in order to facilitate the removal of the *Trichodesmium* colonies coming up to the surface. After 3 to 6 min, colonies were removed using a micropipette and transferred into a 210 ml glass flask previously filled with the same seawater filtered through a Whatman GF/F filter. The water in the pails was gently stirred every 2 or 3 min to prevent colonies from sticking to the walls, which causes a rapid degradation of the cells. Incubations were carried out in a temperature-controlled laboratory (with mean temperature of 26.0 ± 0.2°C during incubations). The glass flask containing colonies was gently shaken with a magnetic agitator. The flask was closed with a silicone stopper equipped with a microelectrode (Clark type, Unisense) fitted to measure the change in O_2 concentration continuously (every 3 s), with a 90% response time of 1 s. The flask was illuminated with 2 light projectors (Osram HLX Xenophot lamp) controlled by a light variator previously calibrated manually for the required intensities using a Biospherical quantum scalar meter QSP-2000. The glass flask was kept in total darkness during the first 5 min of incubation, and then the light intensity (*I*) was progressively increased every 5 min over the range of 0 to 2200 µE m^{-2} s^{-1} (12 to 20 different intensities by experiment), and oxygen production was recorded. The duration of incubation ranged between 75 and 110 min, and the flask content was filtered onto a GF/F filter in order to obtain chl *a* content via spectrofluorometric analysis.

Analysis of photosynthesis vs. irradiance curves. To calculate the *PB* vs. *I* curves and the different photosynthetic parameters, the data points were fitted to an exponential model with the photoinhibition parameter proposed by Platt et al. (1980), using the following algorithms:

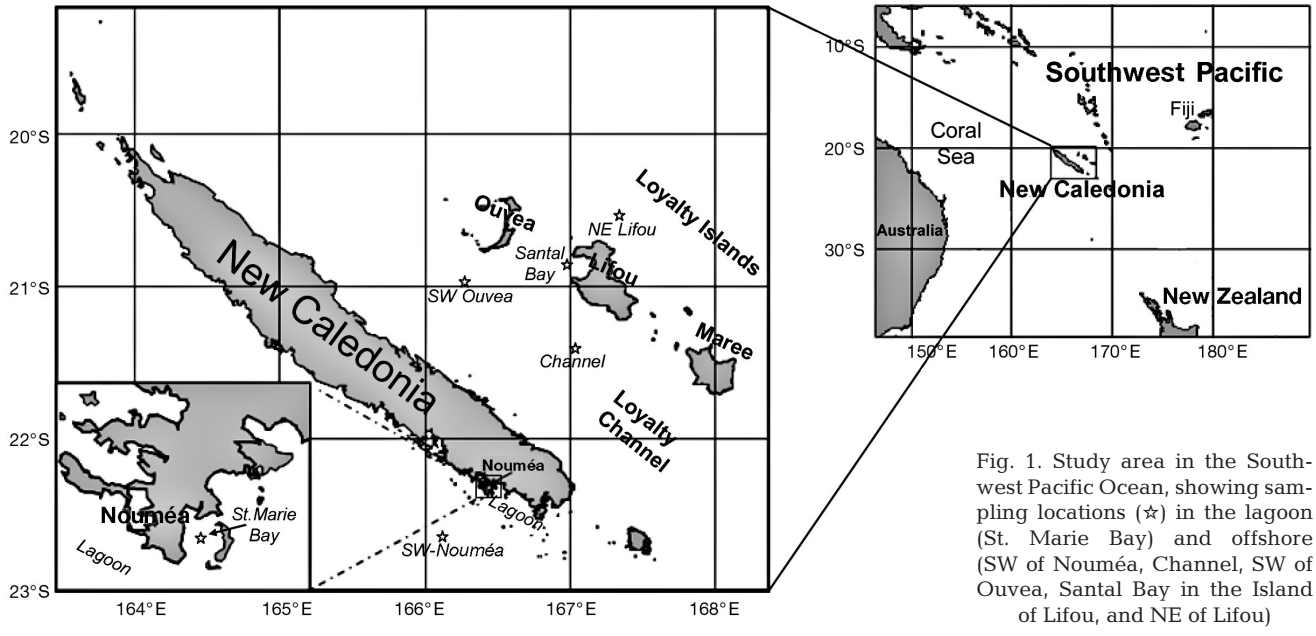

Fig. 1. Study area in the Southwest Pacific Ocean, showing sampling locations (☆) in the lagoon (St. Marie Bay) and offshore (SW of Nouméa, Channel, SW of Ouvea, Santal Bay in the Island of Lifou, and NE of Lifou)

$$PB = \{P_s[1 - \exp(-\alpha I/P_s)][\exp(-\beta I/P_s)]\} - R \quad (1)$$

$$P^B_{max} = P_s[\alpha/(\alpha + \beta)][\beta/(\alpha + \beta)]^{\beta/\alpha} \quad (2)$$

where P_s is the scaling parameter defined as the maximum potential light-saturated photosynthetic rate; α is the photosynthetic efficiency measured by the initial slope of the *PB* vs. *I* curve; β is the photoinhibition index and characterizes the negative slope of the curve for high light irradiances (Platt et al. 1980); *R* is the rate of dark respiration, which was added to Platt's equation to obtain the net photosynthesis; P^B_{max} is the maximum photosynthetic rate, equivalent to P_s when β = 0; I_k is the irradiance saturation parameter, defined as irradiance at the junction of the initial slope and P^B_{max}; and I_c is the irradiance compensation point and was calculated by setting *PB* = 0 in Eq. (1). All rates were normalized to the chl *a* content of the colonies.

Measurement of the photosynthetic quotient in the laboratory. The photosynthetic quotient (PQ) was measured during 30 specific experiments conducted between 19 November and 12 December 2003, using the oxygen method with the addition of a ^{14}C tracer. ^{14}C-bicarbonate (185 kBq) was injected into the 210 ml glass flask through the stopper adapted to the O_2 microelectrode. Experimental conditions were similar to those of the *PB* vs. *I* experiments, except that light intensity was fixed at 1000 µE m^{-2} s^{-1}. Incubation duration was 1 h and O_2 concentration was recorded every 10 s. During the first 5 min of incubation, colonies were exposed to a low light intensity (200 µE m^{-2} s^{-1}), in order to verify the good physiological state of the cells. After incubation, samples were processed as for *in situ* ^{14}C production measurements (see below). The chl *a* content was measured in duplicate 210 ml samples.

***In situ* and simulated *in situ* primary production measurements.** *In situ* measurements were carried out during DIAPALIS cruises as part of the DIAPAZON programme (DIAzotrophy PAcific ZONe, 2001 to 2003). The data used here corresponded to the period from December 2001 to October 2003 and to sampling locations in the vicinity of New Caledonia (Southwest of Nouméa) and around the Loyalty Islands (Loyalty Channel, Southwest of the Island of Ouvea; Santal Bay, in the Island of Lifou; and north-east of Lifou; Fig. 1). Seawater for *in situ* production measurements was collected between 04:00 and 04:30 h, using a rosette of twelve 8 l Niskin bottles. Sampling depths were positioned every 5 m between the surface and 20 m depth, and then every 20 m down to a depth of 100 or 120 m. New sterile 265 ml plastic bottles were gently filled directly from the Niskin bottle tap. The tracer solution was prepared according to the procedure recommended by Fitzwater et al. (1982), and 185 to 370 kBq of ^{14}C-bicarbonate were added to each experimental bottle. For each experiment, 1 to several samples were inoculated with ^{14}C solution and immediately filtered in order to determine incorporation of abiotic particulate ^{14}C. The *in situ* array was launched before sunrise and picked up at about 18:00 h. After incubation, samples were collected on 25 mm GF/F filters using a vacuum pressure of <50 hPa. Duplicate samples were fractionated onto 10 µm polycarbonate filters by gravity alone. Filters were then processed and counted on a liquid scintillation counter according to the procedure described in detail by Le Bouteiller et al. (2003).

Experiments under simulated *in situ* conditions were conducted under natural light using an incubator made of Acrylite 625-5 blue Plexiglas to reduce light intensity to 30% of photosynthetically available radiation (PAR). The incubator temperature was regulated by a circulating water system. Between 6 and 10 replicate samples were taken for each experiment using new 125 ml sterile plastic flasks; 18.5 kBq of ^{14}C-bicarbonate were added, and incubation time ranged from 30 min to 5 h. After incubation, samples were processed as for *in situ* incubations.

Pigments. For *in situ* experiments using the material from the DIAPALIS cruises, 265 ml seawater samples were filtered onto GF/F filters (25 mm in diameter) for total pigment analysis, while 577 ml were collected for size fractionation onto 10 µm polycarbonate filters. After filtration, the filters were stored in cryotubes and kept in a liquid nitrogen container. For pigment extraction, GF/F filters were dipped in a centrifuge tube containing 5 ml of 93% acetone (the final concentration was approximately 90%, after taking into account water retention in the filter), ground with a freshly broken end of a glass rod, and left in the dark at 4°C for a 12 h extraction. Polycarbonate filters were simply left in the dark at 4°C for 24 h in 5 ml of 90% dimethyl formamide. Following extraction, the tubes were centrifuged for 5 min at a speed of 3500 rpm, and the fluorescence of the extracted material was measured with a HITACHI® F4500 spectrofluorometer. Concentrations of chlorophyll pigments, such as monovinyl-chl *a*, -chl *b* and -chl *c* (*c*1 + *c*2; *c*3), divinyl-chl *a* and -chl *b* and phaeopigments derived from these different chlorophylls, were assessed using a modified version of Neveux & Lantoine's (1993) method described by Tenório et al. (2005) and Neveux et al. (2006). Only total chl *a* (the sum of monovinyl- and divinyl-chl *a* concentrations) will be considered here. The procedure for pigment analysis was similar for laboratory and simulated *in situ* experiments, but the sample volume was adapted to the chlorophyll content.

***Trichodesmium* counts.** To compare the pigment content with the *Trichodesmium* abundance during the DIAPALIS cruises, the contents of two 8 l Niskin bottles were entirely filtered in parallel: one for pig-

ment analysis (see above) and the other for cell counts. *Trichodesmium* filaments were generally collected at 4 depths between 0 and 60 m by in-line gravity filtration onto 10 µm-pore size polycarbonate filters (47 mm in diameter). The filters were introduced into glass vials (25 ml) and immediately fixed by addition of a 4% formalin solution. In the laboratory, *Trichodesmium* filaments were recovered by washing the filters with filtered seawater and preserved with 0.4% acid formaldehyde solution. *Trichodesmium* filaments were counted in the whole chamber at a magnification of 100× using an inverted microscope (Olympus IM) following the Utermöhl (1958) technique.

Particulate carbon. Aliquots (5 ml in triplicate) of concentrated *Trichodesmium* cells were directly filtered onto 25 mm GF/F filters for pigment analysis and onto precombusted GF/F filters for POC analysis. The latter filters were dried at 40°C for 24 h and later kept frozen at –20°C until analysis. The POC concentration was determined on a Perkin Elmer 2400 CHN analyzer.

RESULTS

Photosynthesis vs. irradiance and photosynthetic quotient

Among the 7 experiments performed with natural populations of *Trichodesmium erythraeum*, 4 *PB* vs. *I* curves showed a progressive increase in production (*P*) with increasing *I*, reaching a maximum value (P^B_{max}) at a mean PAR irradiance of about 1000 µE m^{-2} s^{-1}, followed by a fall in production at higher light intensity (photoinhibition). Three other curves did not exhibit any evidence of photoinhibition (Fig. 2). The P^B_{max} range (15.2 to 34.8 mg O_2 mg chl a^{-1} h^{-1}; Table 1) is similar to values previously reported for the Atlantic

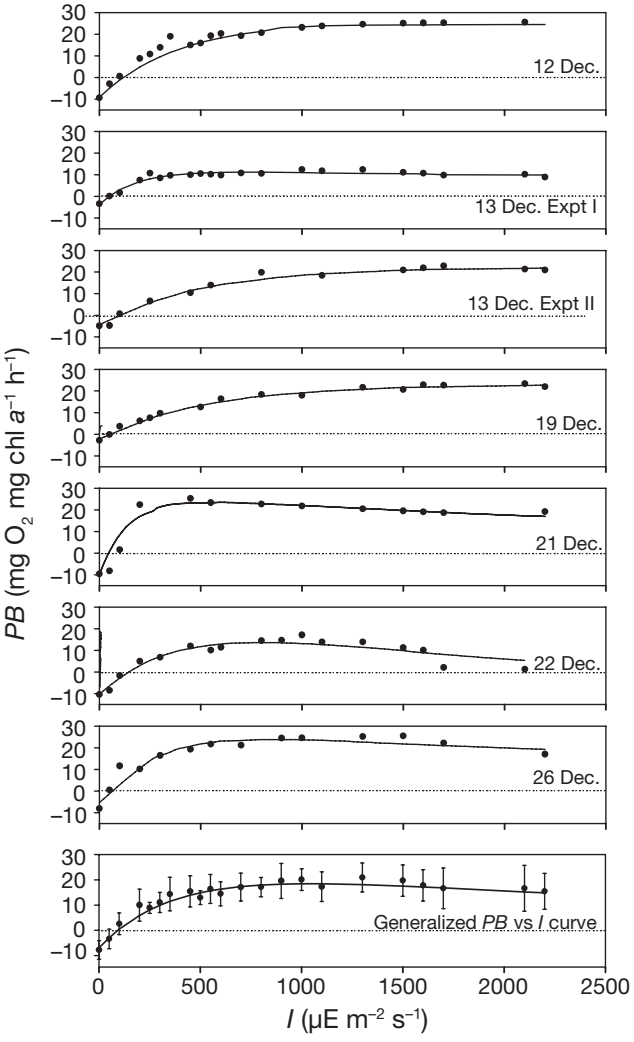

Fig. 2. *Trichodesmium erythraeum*. Photosynthesis vs. irradiance (*PB* vs. *I*) curves; 7 curves were fitted from data points (●) using Platt et al.'s (1980) model. The generalized *PB* vs. *I* curve was fitted using average values of all data

Table 1. *Trichodesmium erythraeum*. Photosynthesis parameters estimated by means of the model of Platt et al. (1980) using 7 photosynthesis (*PB*) vs. irradiance (*I*) curves (Fig. 2). nd: not detected; see Eqs. (1) & (2) in 'Materials and methods' for definitions of parameters

Date	α (mg O_2 mg chl a^{-1} h^{-1} µE m^{-2} s^{-1})	I_k (µE m^{-2} s^{-1})	I_c (µE m^{-2} s^{-1})	R (mg O_2 mg chl a^{-1} h^{-1})	β (mg O_2 mg chl a^{-1} h^{-1} µE m^{-2} s^{-1})	P^B_{max} (mg O_2 mg chl a^{-1} h^{-1})
12 Dec	0.09	392	62	9.1	nd	34.8
13 Dec Expt I	0.09	169	48	3.7	0.001	15.2
13 Dec Expt II	0.06	461	93	4.9	nd	26.9
19 Dec	0.05	475	55	2.8	nd	25.6
21 Dec	0.25	135	63	9.7	0.006	34.0
22 Dec	0.09	452	160	10.4	0.019	31.5
26 Dec	0.16	206	57	8.1	0.005	33.6
Mean	0.12	327	77	7.0	0.008	28.8
SD	0.07	151	39	3.1	0.008	7.0
Generalized *PB* vs. *I* curve	0.08	327	94	6.9	0.007	27.8

Ocean (Carpenter et al. 1993). Most of the experiments presented a P^B_{max} for PAR close to 1000 µE m^{-2} s^{-1}, and one curve exhibited a P^B_{max} for PAR of 450 µE m^{-2} s^{-1}. These P^B_{max} values attained under strong irradiance suggest high light requirements in order to reach maximum values of photosynthesis. All experiments presented a consumption of oxygen in the dark due to respiration (R). R values ranged from 2.8 to 10.4 mg O_2 mg chl a^{-1} h^{-1} (Table 1). The light compensation index ($P = R$) was observed for PAR ranging from 48 to 160 µE m^{-2} s^{-1}. The ranges of values showed that these R and P rates can change from day to day (Fig. 2). R seemed to be directly related to P^B_{max} (Fig. 3). The decrease in production at a PAR >1600 µE m^{-2} s^{-1} showed that photoinhibition can be relatively intense, up to 80% of P^B_{max}. These observations suggest that, paradoxically, photoinhibition would be relatively frequent in *T. erythraeum* present in surface waters.

Thirty experiments using natural *Trichodesmium erythraeum* colonies were performed under fixed conditions of temperature (26°C) and irradiance (1000 µE m^{-2} s^{-1}). Oxygen production and carbon fixation measured together on the same samples were closely correlated ($R^2 = 0.88$). Data were best fitted with a linear regression (Fig. 4) with a slope of 1.191 (mol O_2 mol CO_2^{-1}), which corresponded to the PQ.

The productivity varied slightly with time in the laboratory, *PB* values being first higher and then lower than 4 mg C mg chl a^{-1} h^{-1} from the beginning to the end of the series (Fig. 5a). The mean calculated with all *PB* data was 4.4 mg C mg chl a^{-1} h^{-1} (SD = 1.3, n = 30), with a range between 1.62 and 6.36 mg C mg chl a^{-1} h^{-1}.

Photosynthesis under simulated *in situ* conditions

Experiments performed with *Trichodesmium* under simulated *in situ* conditions (30% of incident PAR) displayed maximum *PB* values after midday when PAR exceeded 300 µE m^{-2} s^{-1}, and lower values in the early morning and late afternoon when PAR ranged from 100 to 200 µE m^{-2} s^{-1} (Fig. 5b). Hence, *PB* was observed to be maximised for about 9 h, i.e. almost 60% of the

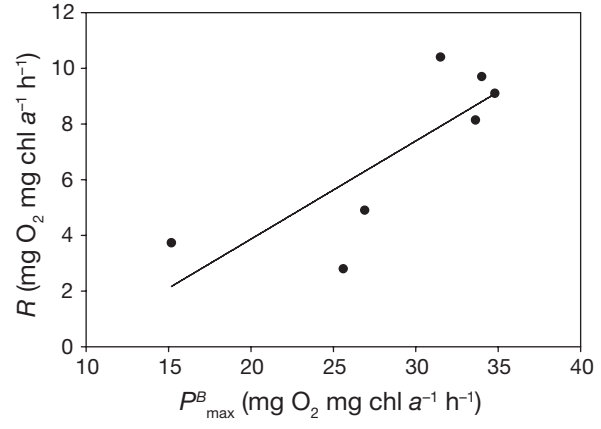

Fig. 3. *Trichodesmium erythraeum*. Variations in dark respiration (R) with maximum photosynthesis (P^B_{max})

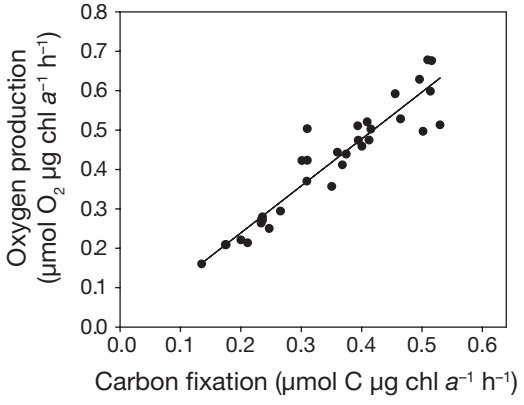

Fig. 4. *Trichodesmium erythraeum*. Variations in photosynthetic oxygen production with carbon fixation rate. Slope of the linear regression is photosynthetic quotient PQ (1.19 mol O_2 mol CO_2^{-1}; n = 30)

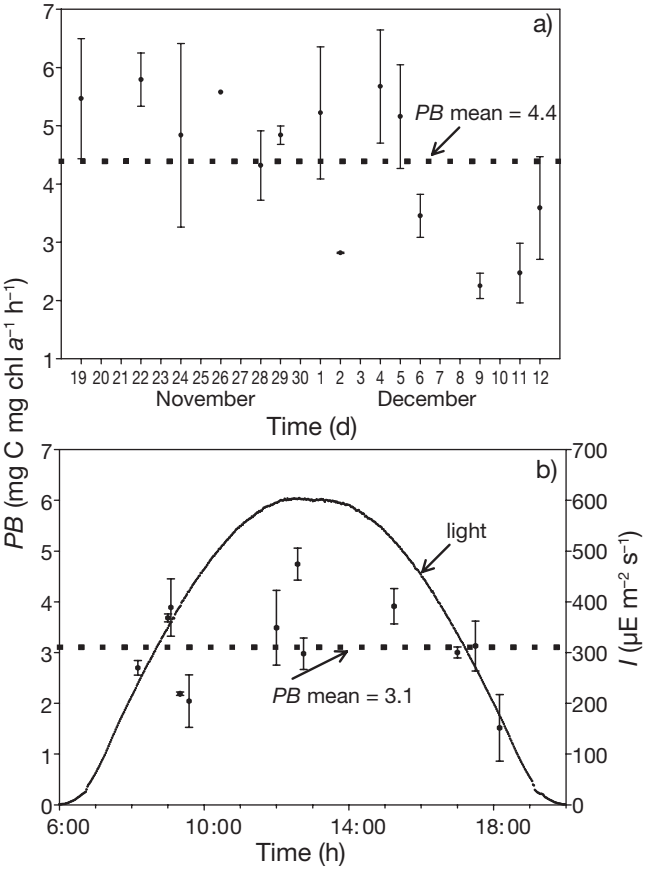

Fig. 5. *Trichodesmium erythraeum*. (a) Daily and (b) mean diel variations in production per unit biomass *PB*

summer daytime period. The mean of all *PB* data (n = 48) was 3.1 mg C mg chl a^{-1} h^{-1} (SD = 0.94), and maximal *PB* was 5.1 mg C mg chl a^{-1} h^{-1}.

C:chl *a* ratio

The mean C:chl *a* ratio measured from concentrated aliquots (in triplicate) of *Trichodesmium erythraeum* colonies collected at the sea surface was 188 g C g chl a^{-1} (SD = 52, n = 11 samples). This C:chl *a* ratio is especially important when calculating growth rate in terms of carbon from CO_2 fixation and chlorophyll content of *Trichodesmium* cells.

Photosynthesis under *in situ* conditions

Trichodesmium abundances were determined in summer (February) at 4 depths (0, 20, 40 and 60 m) and at 4 locations (Santal Bay, north-east of Lifou, Southwest of Ouvea and Southwest of Nouméa) and in winter (August) at 4 depths (0, 20, 50 and 80 m) at 2 locations (Santal Bay and Loyalty Channel) (Fig. 1). In summer, the mixed layer was shallow (ca. 40 m), and abundances were on average 2390 trichomes l^{-1} (SD = 1400, n = 16) in the upper water column (0 to 40 m) and about 2-fold lower at 60 m. The maximum value was observed at the Southwest Ouvea station (4578 trichomes l^{-1}) (Fig. 6a). In winter, the mixed layer was generally deep (100 or 120 m) and abundances ranged from 38 to 76 trichomes l^{-1} (Fig. 6c). In the >10 µm size fraction (or Trichos biomass; Fig. 6), which mainly comprised *Trichodesmium* trichomes and colonies in such waters (J. Neveux pers. comm.), the summer chl *a* concentration ranged between 0.010 and 0.260 mg m^{-3} in the first 40 m (Fig. 6b). The percentage of chl *a* in the >10 µm size fraction varied from 9 to 83% of total chl *a* in the upper layer (0 to 40 m) with a mean of 46% (SD = 20%), decreasing to 6% on average at 80 m (Fig. 6b). Such a result suggests a frequent predominance of *Trichodesmium* populations in summer in the upper layer with respect to other phytoplankton species such as *Synechococcus*, *Prochlorococcus* and picoeukaryotes typical of this region, as shown by Le Bouteiller et al. (2003). In winter, chl *a* (>10 µm) remained around 7.5% (Fig. 6d), corresponding to low *Trichodesmium* abundance. Summer experiments showed that, at the 4 locations, *PB* in the >10 µm size fraction generally increased from the surface to depths of 10 or 20 m and then decreased with increasing depth (Fig. 7a). The mean summer maximum *PB* (PBmax) measured *in situ* was 3.3 mg

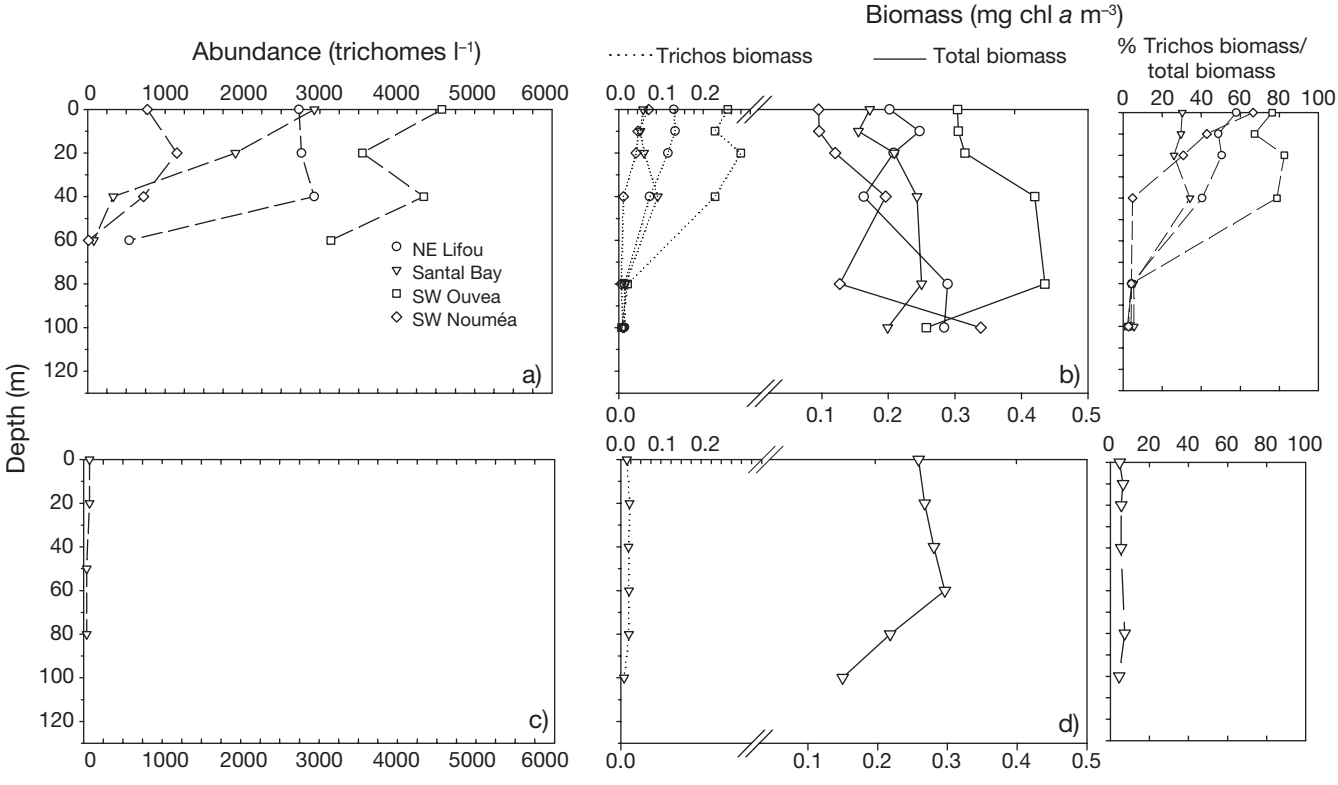

Fig. 6. *Trichodesmium* spp. Abundance and biomass (chl *a* in >10 µm size fraction, Trichos biomass) and total biomass (all phytoplankton) during (a,b) summer (February 2003) and (c,d) winter (August 2002). See Fig. 1 for sampling locations

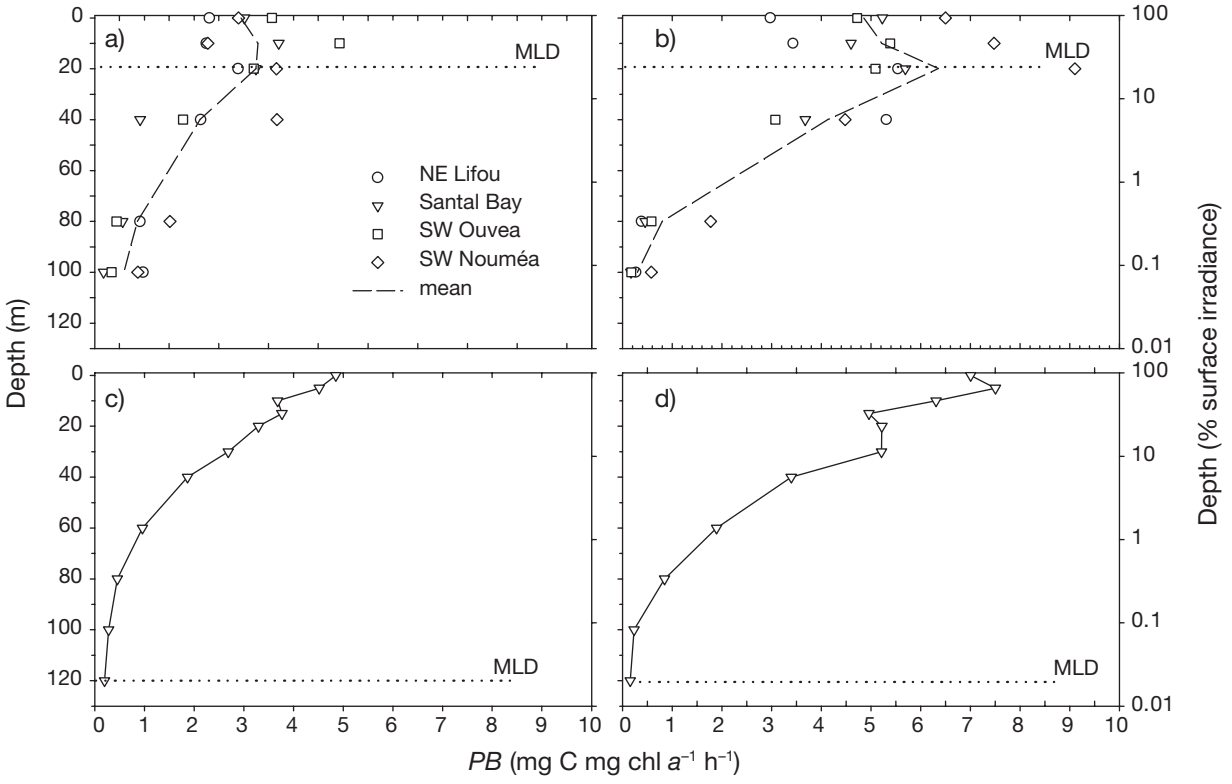

Fig. 7. *In situ* production per unit biomass (*PB*) of *Trichodesmium* and other microphytoplankters in (a,b) summer and (c,d) winter. Mixed-layer depth (MLD; dashed line) was calculated as the depth at which water temperature differed from the sea-surface temperature by 0.4°C (De Boyer Montégut et al. 2004). See Fig. 1 for sampling locations

C mg chl a^{-1} h^{-1} (SD = 0.3, ~20 m depth) for temperatures above 26°C. This PBmax should correspond to the optimal *PB* value for *Trichodesmium* under *in situ* conditions, according to the criteria proposed by Behrenfeld & Falkowski (1997). The relative decrease in *PB* observed at the sea surface, and also at times at 10 m depth, would result from photoinhibition due to excessive available irradiance. This photoinhibition must be compared with the same process observed in the laboratory (Fig. 2). Productivity in the <10 µm size fraction presented the same pattern as in the >10 µm fraction, but *PB* values were significantly higher (mean PBmax = 5.5 mg C mg chl a^{-1} h^{-1}, SD = 0.3) than in the fraction containing *Trichodesmium* (Fig. 7b), as previously observed in the Atlantic Ocean (Carpenter et al. 2004). In winter, *Trichodesmium* productivity (>10 µm fraction) displayed a PBmax of 4.9 mg C mg chl a^{-1} h^{-1} at or near the surface (Fig. 7c). PBmax in the <10 µm fraction varied from 7.0 mg C mg chl a^{-1} h^{-1} at the surface (when mean PAR 0^+ was as low as 1.9 E m^{-2} h^{-1}; Table 2) to 5.0 mg C mg chl a^{-1} h^{-1} at 20 m (Fig. 7d).

Table 2. *Trichodesmium* spp. Optimal production per biomass (*PB* for size fraction >10 µm) in the upper surface layer (0–20 m) during DIAPALIS cruises (2001–2003). *Z*: depth (m)

Date	Location	PAR 0^+ (E m^{-2} h^{-1})	*PB* > 10 µm (mg C mg chl a^{-1} h^{-1})	*Z* (m)	PAR (*Z*) (E m^{-2} h^{-1})
Dec 2001	Santal Bay	4.20	4.0	10	1.47
	Channel	4.25	4.9	20	0.77
Jan 2002	Channel	2.52	7.6	20	0.45
Apr 2002	Channel	2.28	5.0	20	0.41
May 2002	Channel	0.76	3.9	0	0.57
	Channel	0.76	3.6	5	0.38
Aug 2002	Santal Bay	1.91	4.9	0	1.43
	Santal Bay	1.91	4.5	5	0.96
Feb 2003	NE Lifou	3.75	2.9	20	0.49
	Santal Bay	3.20	2.8	20	0.42
	Santal Bay	2.98	2.1	10	1.04
	Santal Bay	3.29	3.7	10	1.14
	SW Ouvea	3.58	4.9	10	1.25
	SW Nouméa	3.49	2.7	0	2.62
	SW Nouméa	3.59	3.7	20	0.47

DISCUSSION

Photosynthesis vs. irradiance and the photosynthetic characteristics of *Trichodesmium*

The photosynthetic characteristics (P^B_{max}, α, R, I_k and I_c) observed in *Trichodesmium erythraeum* in the SWP are not significantly different from those reported for the North Atlantic Ocean (Table 3). R was always relatively high: up to 24 % of the O_2 produced by photosynthesis was consumed by respiration. P^B_{max} and R both exhibited a relatively wide variation (Fig. 3), which might be inherent to process studies involving bottle incubations with variable natural communities of *Trichodesmium*. To perform the numerous experiments, field samples of *Trichodesmium* colonies may differ, for example, by different degrees of photoacclimation, depending on the various light regimes experienced previously by colonies. For instance, just before being sampled, some *Trichodesmium* colonies could have risen to the surface from depth by positive buoyancy (Walsby 1992), and the photosynthetic responses of such colonies are likely to differ from those of cells strongly photoacclimated to the strong irradiance in the upper water column.

Furthermore, the *Trichodesmium* respiration rate is known to present a marked circadian rhythm (Kana 1993, Roenneberg & Carpenter 1993), which could have affected results because the *PB* vs. *I* experiments were performed at different times in the morning. The low but significant correlation between R and P^B_{max} (Fig. 3) suggests that the cyanobacteria that exhibit the strongest photosynthetic capacities also have the highest respiration rate, as previously shown by Carpenter et al. (1993). Conceptually, the most photosynthetically efficient organisms, which are probably not nutrient-limited and are almost perfectly photoacclimated to the experimental conditions, would exhibit the highest respiration rate, suggesting that this intense respiration was required for optimal growth. Since rapid oxygen cycling in *Trichodesmium* may contribute to the protection of nitrogenase from excess O_2 and simultaneously provide biochemical energy required for nitrogenase activity (Kana 1993), one may suggest that the highest photosynthetic capacities would correspond to the highest levels of diazotrophic activity.

The mean PQ obtained under saturating irradiance with natural *Trichodesmium erythraeum* colonies (Fig. 4) was 1.19 mol O_2 mol CO_2^{-1} (SD = 0.13, n = 30). According to Laws (1991), changes of PQ from 1.1 to 1.4 are a function of the N source for phytoplankton: the highest values reflecting a preference for NO_3, and the lowest a preference for NH_4. Hence, the mean PQ value found here would correspond to a slight predominance of NH_4 uptake, which is in agreement with observations reported by Mulholland & Capone (1999) that suggest that *Trichodesmium* communities would have a high affinity for NH_4. This PQ of 1.19 is similar

Table 3. *Trichodesmium*. Comparative photosynthetic parameters values in the Atlantic and Pacific Oceans. 'Other species' corresponds to *T. thieubauti* and *Trichodesmium* spp. SD: standard deviation; ~: no data; *: *in situ PB* values of *Trichodesmium* spp.

Parameter	Atlantic Ocean		Pacific Ocean			
	Bahamas - Eastern Caribbean, Sargasso Sea and Belize		North Pacific	South Pacific		
				Timor & Arafura Seas	New Caledonia (this study)	
	Other species Range	*T. erythraeum* Mean (SD)	Other species Range	Other species Range	*T. erythraeum, T.* spp.* Range	Mean (SD)
P^B_{max} (mg O_2 mg chl a^{-1} h^{-1})	6.45[a]–65.7[b]	36.9 (18.4)	~	~	15.2–34.8	28.8 (7.0)
α (mg O_2 mg chl a^{-1} h^{-1} µE m^{-2} s^{-1})	0.019[e]–0.27[b]	0.11 (0.07)	~	~	0.05–0.25	0.12 (0.07)
R (mg O_2 mg chl a^{-1} h^{-1})	4.9[a]–24.9[c]	24.9 (5.2)	~	~	2.8–10.4	7.0 (3.1)
I_k (µE m^{-2} s^{-1})	142[a]–687[c]	324 (216)	~	~	135–475	327 (151)
I_c (µE m^{-2} s^{-1})	30–325[d]	~	~	~	48–160	77 (39)
β (mg O_2 mg chl a^{-1} h^{-1} µE m^{-2} s^{-1})	~	~	~	~	0.001–0.019	0.008 (0.008)
C assimilation (*PB*, mg C mg chl a^{-1} h^{-1})	0.2–5[f]	~	0.38[g]–5.2[h]	0.3–4.5[i]	Laboratory 1.6–6. 4 Simul. *in situ* 0.6–5.1 *In situ** 0.2–7.6	4.4 (1.3) 3.1 (0.9) 3.3 (0.3)

[a]Carpenter & Roenneberg (1995); [b]Roenneberg & Carpenter (1993); [c]Carpenter et al. (1993); [d]Daily variability of I_c, in Kana (1993); [e]Villareal (1995); [f]Carpenter et al. (2004); [g]Mague et al. (1977); [h]Shimura et al. (1978); [i]Berman-Frank et al. (2001)

to the value of 1.2 that is commonly accepted as typical for most phytoplankton (Laws 1991). However, this value of PQ is nearly 2-fold higher than those reported by Carpenter & Roenneberg (1995) for *Trichodesmium* spp. in the Caribbean Sea. The PQ may be influenced by excretion of C and N (Laws 1991); however, we did not measure excretion in the present study. If not due to a difference in experimental protocol, such a discrepancy is difficult to account for without more information.

In situ primary productivity of *Trichodesmium*

In the open SWP, the vertical profiles of *in situ* primary productivity for the >10 µm size fraction containing *Trichodesmium* trichomes and colonies exhibited PBmax values that ranged from 2 to 7.6 mg C mg chl a^{-1} h^{-1} (Table 2). Photoinhibition (ca. 10% of PBmax) affected *Trichodesmium* photosynthesis in the upper water column, as determined from PAR values (Fig. 7a) that, when averaged over the daytime, exceeded about 500 µE m^{-2} s^{-1}. This photoinhibition decreased or completely vanished in cloudy weather, especially in winter (Fig. 7c). As a consequence, PBmax generally occurred at about 20 m depth and rose towards the surface in response to any occasional decrease in the incident irradiance. The climatological variations of PAR present a maximum/minimum seasonal amplitude of 1.4 at the latitude of the studied region (21 to 22° S). Clearly, the photoinhibition evidenced both *in situ* and in the laboratory (Fig. 2) might dramatically affect the massive surface accumulations of *Trichodesmium* during blooms. In summer, as in winter, all the vertical profiles of productivity showed the same pattern, with a regular decrease in *PB* values from PBmax to the bottom of the euphotic layer, whose depth varied between 60 and 95 m (Fig. 7a,c). Much the same range of values and the same variation in productivity were observed in *Trichodesmium* during a series of 3 cruises in the tropical North Atlantic (Carpenter et al. 2004). Similar *PB* values were also reported from 2 days of experiments on *T. erythraeum* colonies conducted in the Timor and Arafura Seas in the western equatorial Pacific (Berman-Frank et al. 2001).

The similarity between *in situ* and simulated *in situ* productivity values suggests that, in spite of different environments (lagoon and open-ocean) and species, all *Trichodesmium* populations present equivalent photosynthetic performances in the region. The mean PBmax value (3.3 mg C mg chl a^{-1} h^{-1}, SD = 0.3) from *in situ* incubations did not differ significantly from results of simulated *in situ* experiments (PBmax = 3.1 mg C mg chl a^{-1} h^{-1}, SD = 0.9), whereas laboratory experiments produced a slightly higher mean PBmax (4.4 mg C mg chl a^{-1} h^{-1}, SD = 1.3) under optimal light and temperature conditions. PBmax observed *in situ* would correspond to the *Trichodesmium* optimal productivity under favourable light conditions, following Behrenfeld & Falkowski's (1997) criteria. All these results lead to the conclusion that the photosynthetic capacities of *Trichodesmium* do not differ significantly between the Atlantic and the Pacific, and appear to be characteristic of this genus. In the future it would be interesting to consider these particular photosynthetic characteristics in the ocean models that include *Trichodesmium* and N_2 fixation, as well as in models of carbon and nitrogen cycles.

The optimal *PB* of *Trichodesmium* measured in the >10 µm size fraction (Fig. 7a,c) was generally lower than the *PB* of the <10 µm fraction, containing nano- and picoplankton communities (Fig. 7b,d). This small fraction is mainly composed of *Synechococcus*, *Prochlorococcus* and picoeukaryotes, whose distributions in the western tropical Pacific have been described in detail by Le Bouteiller et al. (1992). The difference in PBmax between the >10 and <10 µm fractions may be compared with observations made in the North Atlantic: using quite different experimental procedures, Carpenter et al. (2004) found that the PBmax values of isolated *Trichodesmium* colonies were 2 to 4 times lower than PBmax measured in samples without colonies. They suggested that, in spite of *Trichodesmium*'s active photosynthesis, a relatively low PBmax could be due to a weak efficiency of carbon metabolism and assimilation. This low efficiency could result from a strong excretion rate (Li et al. 1980) or a high respiration rate (Kana 1993). However, other causes of variability may explain low *PB*.

According to Laws & Wong (1978), *PB* may be written as the product of the fractional rate of increase in cellular C and the C:chl *a* ratio:

$$PB = (1/C \times dC/dt)(C/\text{chl } a)$$

where C is the cell carbon content in *Trichodesmium*. On average, the term '$1/C \times dC/dt$' can be approximated by the growth rate (µ). Assuming that the C:chl *a* ratio is more or less equal in all phytoplankton subjected to the same light regime in the upper water column, then *PB* would be positively correlated with growth rate. In the SWP, the mean C:chl *a* ratio of *Trichodesmium* sampled at the sea surface was 188 g C g chl a^{-1} (SD = 52), which is not significantly different from the C:chl *a* ratio estimated for the <3 µm size fraction at the sea surface in the western equatorial Pacific by Le Bouteiller et al. (2003) (144 g C g chl a^{-1}, SD = 40). As reflected by lower PBmax, *Trichodesmium* would have a slower growth rate than the other phytoplankters. In the SWP, the *Trichodesmium* growth rate was estimated as ranging between 0.18 and 0.32 d^{-1}

(mean 0.21 d^{-1}) in optimal light conditions, whereas μ in phytoplankton as a whole averaged 0.55 d^{-1} at subsurface depths in the western equatorial Pacific (Le Bouteiller et al. 2003).

High light requirements for *Trichodesmium* growth

Under simulated *in situ* conditions, the productivity of *Trichodesmium* was maximised when PAR exceeded 300 μE m^{-2} s^{-1} (Fig. 5b). This irradiance is in agreement with the photosynthetic saturation parameter (I_k = 327 μE m^{-2} s^{-1}, SD = 151) obtained from *PB* vs. *I* experiments with *T. erythraeum* (Table 1). This mean I_k value is similar to those reported for *Trichodesmium* in previous studies conducted in the Atlantic Ocean (see Table 3; Carpenter et al. 1993, Carpenter & Roenneberg 1995). Typically, this I_k value is much higher than the I_k for cultures of *Synechococcus* (range 77 to 130; Glover et al. 1987), for *Prochlorococcus* (range 40 to 80; Moore & Chisholm 1999) and for picoeukaryotes (range 143 to 267; Glover et al. 1987). Field data may be used to determine at what depths such light levels are observed in the studied region. At the latitude of the study and in clear weather, the mean incident daytime irradiance PAR 0^+ ranges between ~625 and 1200 μE m^{-2} s^{-1} in winter and summer respectively. Taking these changes into account and assuming a constant mean incident radiation throughout the daytime, the mean optimal PAR of 300 μE m^{-2} s^{-1} was estimated (depending on the range of potential euphotic layer depths, which could vary from 60 to 95 m) to be available at depths between 10 and 20 m in winter, and between 15 and 25 m in summer. Thus, in fine weather, the optimal depth for *Trichodesmium* photosynthesis in the region would be between 10 and 25 m. In cloudy weather, and depending on cloud-cover intensity and duration, this optimal light level becomes more shallow, eventually occupying the surface. *In situ* measurements showed that the PBmax of *Trichodesmium* was systematically observed at or above a depth of 20 m, exactly as expected from results of simulated *in situ* and laboratory experiments.

As for I_k, the depth at which the available solar radiation equalled I_c was estimated in the water column. I_c was chosen as the lowest value found in the SWP (I_c = 48 μE m^{-2} s^{-1}; Table 1, 13 December, Expt I). Hence, the depth at which O_2 consumption by *Trichodesmium* respiration equals O_2 production by photosynthesis is the compensation depth, and was conservatively estimated to range between 20 m in winter, in the case of a shallow euphotic zone (60 m), and 55 m in summer, when the euphotic zone was deepest (95 m). The application of the results of *PB* vs. *I* experiments to field observations leads us to conclude that the maximum depth of the photosynthetic layer for *Trichodesmium* is quite shallow, even without any cloud cover, and is most often between depths of 40 and 50 m. These results suggest that *Trichodesmium* would not present any significant growth below a specific compensation depth situated well above the compensation depth of most other typical tropical phytoplankton species, which is classically defined as the bottom of the euphotic layer.

Field data showed that, in agreement with their photosynthetic characteristics, *Trichodesmium* generally predominated in the top 20 or 30 m layer, as also observed in the Atlantic (Carpenter et al. 2004). However, colonies were at times observed to be relatively abundant at depths of 40 m or even 60 m (Fig. 6a), i.e. at the level of or quite below the compensation depth, which is also close to the bottom of the mixed layer in summer. Although no acclimation was demonstrated at depth during the same field study (Neveux et al. 2006), some acclimation may occur in *Trichodesmium* colonies, allowing them to photosynthesize under conditions of low PAR. This hypothesis is supported by *in situ* observational data that indicated that a significant carbon fixation in the >10 μm fraction occurred at 80 m or even 100 m depth (Fig. 7a,c). However, this carbon fixation does not necessarily signify a positive net carbon production. The extremely low photosynthetic rate detected under a very dim light regime probably does not allow *Trichodesmium* to sustain any significant development of populations at a depth close to the bottom of the euphotic zone, and hence would not have any effect in the food web.

In some cases, and in spite of their potential positive buoyancy (Walsby 1992), some colonies could have been swept downward by eddy-induced convergent motions related to the circulation of the South Equatorial Current, which flows over or among the numerous seamounts and islands of the New Caledonian archipelago. Similarly, *Trichodesmium* colonies have been detected at depth in cyclonic eddies of the Atlantic Ocean (Davis & McGillicuddy 2006). In addition, variable buoyancy has been put forward to explain how *Trichodesmium* colonies could migrate through the water column (Walsby 1992), possibly in order to mine nutrients abundant at the depth of the nutricline (Letelier & Karl 1998). However, *Trichodesmium* colonies were generally observed to be scarce or totally absent at 80 m in the SWP, precisely at a depth where phosphate generally appears in the region (Moutin et al. 2005). On the contrary, its admittedly strong energy requirements force *Trichodesmium* to stay in the upper water column. Only the organisms present in this upper layer would have the capacity to succeed in cellular division in adequate time to maintain or improve the population. Furthermore, results of the present

study are in agreement with most previous field studies in considering that the *Trichodesmium* growth rate, even under the best light regime, is typically slow, with at best 1 cellular division every 2 or 3 d. Therefore, such a slow growth rate determines the time-scale of the population dynamics of *Trichodesmium*. To be able to proceed with cell division, *Trichodesmium* colonies require a strong incident radiation; in addition, such energy must be available for a long time, enough for cell division to be effective, i.e. at least 2 or 3 consecutive days. That is the reason why the vertical stratification of the water column is so important for maintaining *Trichodesmium* at the optimum light level for a time period sufficient for the necessary photoacclimation and cell division.

Hood et al. (2001) conceived a mathematical model that relates the seasonal variations in *Trichodesmium* concentration to the seasonal changes in both light availability and stratification of the water column. This model was applied to North Atlantic observations, where *Trichodesmium* abundance seems to be effectively higher when the mixed layer is shallower during the summer/early autumn, and where concentrations are much lower in winter/early spring when light availability is low and deep mixing occurs. Such observations suggest that the capacity of *Trichodesmium* to regulate its buoyancy is not sufficient to maintain trichomes at a constant light level in a turbulent mixed layer. In contrast, if the light regime is propitious over an extended time with optimal nutrient availability, cells divide and the *Trichodesmium* population slowly grows, and a gradual development of the biomass occurs. However, in an oligotrophic environment where all auto- and heterotrophic organisms are strongly interdependent, an increase in the biomass of a particular compartment of the food-web is only possible if the growth rate exceeds the loss rate. The loss rate of *Trichodesmium* due to grazing would be highly dependent on biomass, being low when colonies are scarce and potentially high during blooms (O'Neil 1998). In the SWP, concentrations of *Trichodesmium* are relatively low and most *Trichodesmium* is present as free trichomes. Furthermore, the main grazer of *Trichodesmium*, the copepod *Macrosetella gracilis*, has never been observed in the 5 l samples used for counting trichomes (M. Tenório pers. comm.). The loss rate by sedimentation has been observed to be very low in the NW Pacific (Wu et al. 2003) and in the SWP, where neither *Trichodesmium* colonies nor specific pigment traces have been detected in sediment traps deployed during our study (M. Rodier pers. comm.). These observations suggest that, in the SWP, the loss rate due to grazing and sedimentation would be slower than the *Trichodesmium* growth rate, at least when the light regime is optimal in the summer period.

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