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^{13}C and ^{15}N uptake by marine phytoplankton. III. Interactions in euphotic zone profiles of stratified oceanic areas

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ABSTRACT: Upon addition of inorganic nitrogen to phytoplankton in various nutritional states, transient changes in net carbon uptake were observed over a few hours in daylight, both in euphotic zone profiles and in time series of natural and cultured samples. The reductions in carbon fixation, probably due to increased respiration, led to inverse relations between carbon and nitrogen uptake. They were sometimes followed by stimulations of carbon uptake, corresponding or not to exhaustion of the added nutrient. Such phenomena could not be readily interpreted in terms of nutrient deficiency, as they also occurred in waters in which dissolved nitrogen compounds were around 3 μM. Under controlled laboratory conditions, interspecific variability in responses of the carbon uptake system to a nitrogen addition was very high, but the absolute irradiance level appeared to be determinant in the manifestation of such patterns.

INTRODUCTION

Although in eutrophic areas the carbon-to-nitrogen (C/N) composition ratio can sometimes be used as index of the metabolic activity of natural phytoplankton (Collos and Lewin, 1976; Slawyk et al., 1978), this is not the case in oligotrophic areas, where such indices are subject to considerable bias by non-phytoplankton material (Banse, 1974). Another parameter, the C/N uptake ratio (calculated from absolute rates in units of mass volume^{-1} time^{-1}) is not subject to such bias in the field (Dugdale and Goering, 1967). In laboratory cultures, Collos and Slawyk (1979) reported that such a ratio was smaller than the corresponding composition ratio of algal cells upon addition of inorganic nitrogen to previously nitrogen-limited cultures, due to a reduction in net carbon uptake. In non-limited cultures, the uptake ratio was equal to, or greater than, the composition ratio. It therefore appeared acceptable to use the C/N uptake ratio as a diagnostic tool to qualify the nutrient status of natural phytoplankton, taking into account the effect of other factors, such as the irradiance level (Slawyk and Collos, 1978). However, the C/N uptake ratio is hard to estimate accurately in the field because of the difficulty of taking into account all possible nitrogen sources (Slawyk et al., 1978; Slawyk and Collos, 1982). This led us to examine another parameter, independent of biomass, and involving carbon uptake only, i.e. the ratio of carbon uptake with nitrogen addition to carbon uptake without nitrogen addition. This parameter is somewhat similar to the enhancement ratio of Morris et al. (1971), but is a more general case, as it includes eventual reductions in carbon uptake during the light period as well (Fedorov and Semin, 1970; Falkowski and Stone, 1975; Lean and Pick, 1981; Lean et al., 1982; Terry and Caperon, 1982; Turpin, 1983).

The effect of nitrogen addition on carbon uptake by algal cells is currently the subject of considerable controversy, even under controlled laboratory conditions (Goldman and Dennett, 1983; Turpin, 1983), and the response of natural populations is generally much more complex than that of cultures (Lean et al., 1982). Therefore, we tried to employ additional data obtained on laboratory cultures in order to help interpret field results, and to resolve discrepancies concerning interactions between carbon and nitrogen uptake by phytoplankton which are apparent in the literature.

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METHODS

Results presented here were obtained in the Equatorial Atlantic Ocean, off the Ivory Coast between Abidjan and St. Helena Island, in August-September 1978 ('SUPREA' cruise) and in coastal waters off Portugal in September 1981 ('RCA-I' cruise). Samples were taken with 30 l Niskin bottles at standard depths. Seawater was prefiltered through 200 µm mesh. Time-course uptake measurements were carried out to assess the effect of enclosure on the uptake characteristics of the phytoplankton. ^{13}C labeled bicarbonate (10 % of ΣCO_2) and various nitrogen sources labeled with ^{15}N were added to samples of surface water at saturating (10 µgat $N\,l^{-1}$) or trace (0.1 µgat $N\,l^{-1}$) levels, and incubated according to the 'simulated *in situ*' technique (MacIsaac and Dugdale, 1972) at 75 % of surface irradiance for various periods of time ranging from 30 min to 48 h. The effect of nitrogen addition on carbon uptake was examined both in time-course measurements on surface samples and laboratory cultures, and in euphotic zone profiles (n = 5) using 12 h *in situ* incubations (Slawyk et al., 1976). Water samples were spiked with ^{13}C only (control) or with ^{13}C and ^{15}N enrichments (nitrate and/or ammonium) in saturating amounts (4 µgat $N\,l^{-1}$ for ammonium, 9 to 18 µgat $N\,l^{-1}$ for nitrate).

Laboratory cultures of marine diatoms were grown in chemostats at a dilution rate of 0.04 h^{-1} as in Collos and Slawyk (1979) for nitrogen-limited cells, except that the light regime was 12 h light/12 h dark, and as Collos (1980) for nitrogen-starved cells. Light intensity (50 µE $m^{-2}\,s^{-1}$) corresponded to the irradiance level of the thermocline in a stratified oceanic area (Groupe Mediprod, 1977). Temperature was 20 °C ± 1 C°. Natural nutrient-poor seawater collected off Marseille and Millipore filtered was enriched so that inorganic nitrogen was limiting (ca. 10 µgat $N\,l^{-1}$ in the inflow medium). Before uptake experiments, pumping of inflow medium was stopped, and an initial nutrient response measurement was done 3 h after the beginning of the light period.

Carbon and nitrogen uptake was measured after Slawyk et al. (1977, 1979). For field work, the ^{13}C solutions were prepared on board and stored in polyethylene bottles. Their stability was checked by gas chromatography (Oudot and Wauthy, 1978). Nutrient and chlorophyll data are taken from Voituriez (1980) and Groupe Mediprod (1983). We define the carbon uptake response ratio (CURR) as ratio between carbon uptake with nitrogen addition to carbon uptake without nitrogen addition. Values smaller than 1 indicate that net carbon uptake is reduced upon nitrogen addition, while CURR values greater than 1 indicate a stimulation of carbon uptake.

RESULTS

Linearity of uptake in routine incubations

We looked for evidence of significant changes in the uptake characteristics of the phytoplankton during the routine incubations used in this study. A long-term time series of isotope enrichment is presented for Equatorial Atlantic waters (Sta. 59 of SUPREA cruise) for both ^{15}N and ^{13}C (Fig. 1), starting with a light period and lasting 48 h. Significant increases in enrichment

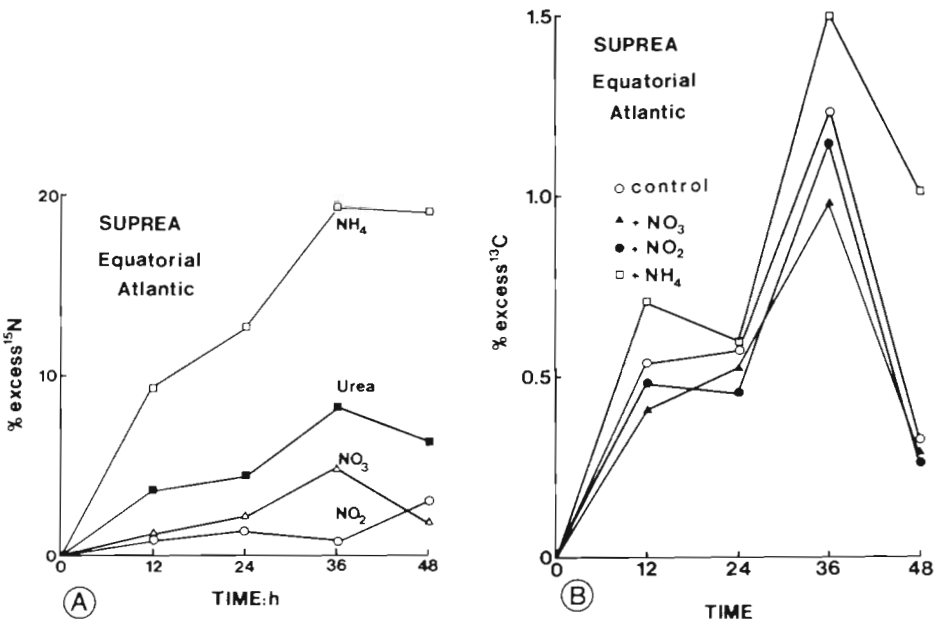

Fig. 1. Long-term time course of (A) ^{15}N enrichments in particulate matter from Equatorial Atlantic surface waters; (B) ^{13}C enrichments in particulate matter from Equatorial Atlantic surface waters

occur during the light period for both ^{15}N (except nitrite) and ^{13}C isotopes, and significant decreases occur during the second dark period, with nitrogen losses ranging from 0.3 to 3 %, and carbon losses from 8 to 18 % of the biomass present at the beginning of the dark period. The only exception to these patterns is the sample enriched with nitrite, whose uptake rate is greater during the second dark period. Small carbon losses (0.5 to 2 %) were also observed during the first dark period for samples with nitrite and ammonium additions.

The slopes of the lines between 2 successive days are not significantly different (except for nitrate, which might have led to induction phenomena in these nutrient-poor waters). This means that the accumulation of isotope, and therefore uptake, remains constant in the incubation bottles.

Short-term (0 to 8 h) time series obtained in the North Atlantic (RCA-1 cruise) off Portugal show regular increases in the incorporation of ^{15}N during incubations (Fig. 2). These results, as well as those presented in Slawyk et al. (1984) concerning ^{13}C uptake, obtained in the same study area, show that uptake was linear with time under the experimental conditions used in this study.

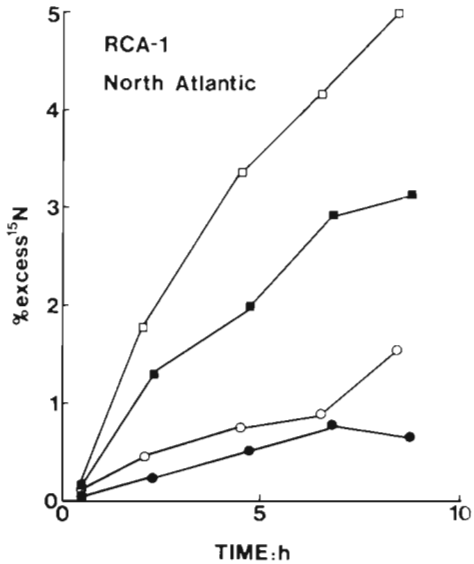

Fig. 2. Short-term time course of ^{15}N enrichments in particulate matter from coastal waters off Portugal

Euphotic zone profile experiments

Surface nutrient and biomass for the 10 stations where uptake measurements were conducted are given in Table 1. Soluble reactive phosphorus and silicate concentrations were always greater than 0.3 and 0.7 µM respectively. Assimilation numbers (AN) ranged from 0.5 to 29.4 mgC mg chl*a* h^{-1}. The latter value is above the theoretical maximum estimated by Falkowski (1981), but should be considered as an overestimate because chl*a* levels are probably too low, due to the presence of accessory pigments (Neveux, 1976) and particularly Chl *c*, which on several occasions was higher than Chl*a* when estimated by the method of Strickland and Parsons (1968).

Nitrogen (N) enrichments led to variable responses in carbon (C) uptake. In the Equatorial Atlantic (Fig. 3), we recorded a significant decrease in C uptake at the surface following a N addition (2-fold for ammonium addition at Sta. 50, to 7-fold for nitrate addition at Sta. 19). This pattern disappeared with depth (Sta. 19 and 50), or was reversed, as some sam-

Table 1. Inorganic nitrogen nutrients and biomass data for Equatorial Atlantic stations (19 to 134) and Northeastern Atlantic stations (P4 and P5)

Station	Z(m)	NO_3	NO_2	NH_4	Chl *a*	Pheo	PC	PN	AN
19	0	2.9	0.09	0.58	0.18	0.17	8.0	1.0	3.9
50	10	3.0	0.09	U	0.38	0.23	7.0	1.1	0.6
59	10	U	U	U	0.12	0.07	7.2	1.2	6.8
83	0	U	U	U	0.50	zero	4.4	0.6	0.5
120	0	U	U	U	0.46	zero	3.9	0.6	0.9
129	0	2.5	0.17	0.90	0.45	0.13	9.8	1.4	0.3
130	0	2.5	0.17	1.00	0.36	0.09	12.0	1.9	29.4
134	0	2.3	0.17	0.80	0.36	0.13	14.1	2.2	16.6
P4	0	U	U	NA	0.29	0.10	NA	1.2	3.6
P5	0	0.1	0.02	NA	0.66	zero	NA	1.6	2.1

Dissolved and particulate nitrogen (PN in µgat N l^{-1})
Particulate carbon (PC in µgat C l^{-1})
Chl *a* and Pheo in µg l^{-1}
Assimilation number (AN) in µgC µg Chl a^{-1} h^{-1}
U: undetectable
NA: not available

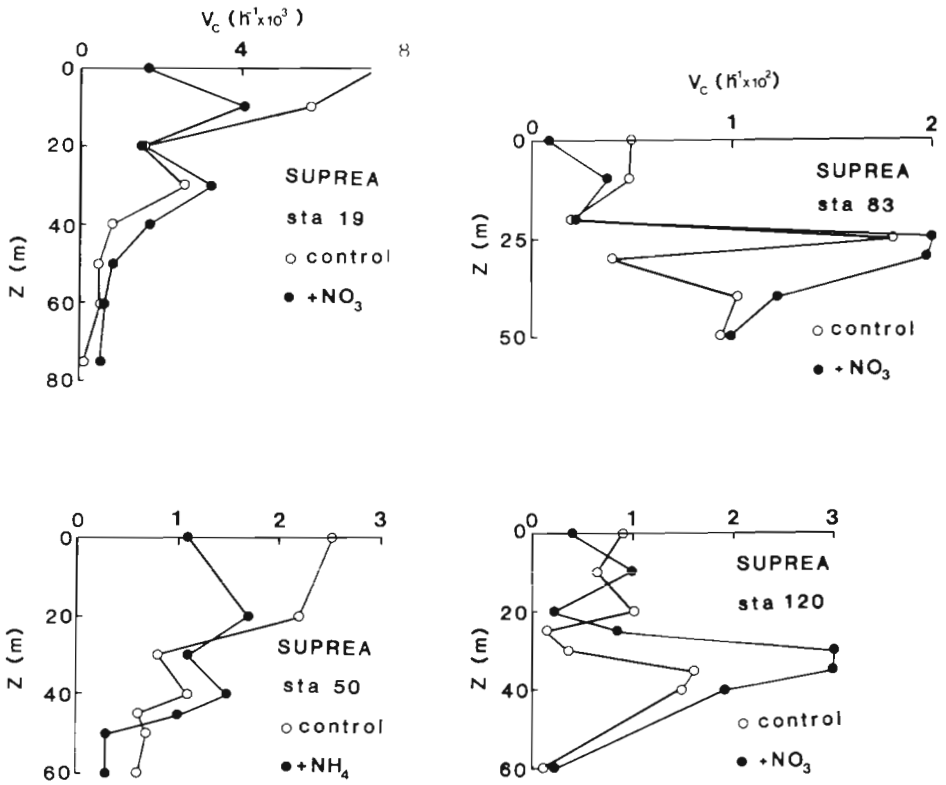

Fig. 3. Effect of nitrogen enrichment on carbon uptake in euphotic zone profiles of the Equatorial Atlantic

ples showed an increase in C uptake when inorganic N was added near the 30 m depth (5-fold at Sta. 83, to 8-fold at Sta. 120). This increase always occurred in the nitracline.

Stimulation of C uptake could also occur in nutrient depleted surface samples (Fig. 4). Values of the carbon uptake response ratio (CURR) are shown in Table 2, along with inorganic N levels for these 5 stations. The CURR ranged from 0.1 to 10, and generally increased (4 out of 5 stations) with depth with maxima in the thermocline for Stations 83 and 120, and then decreased with depth.

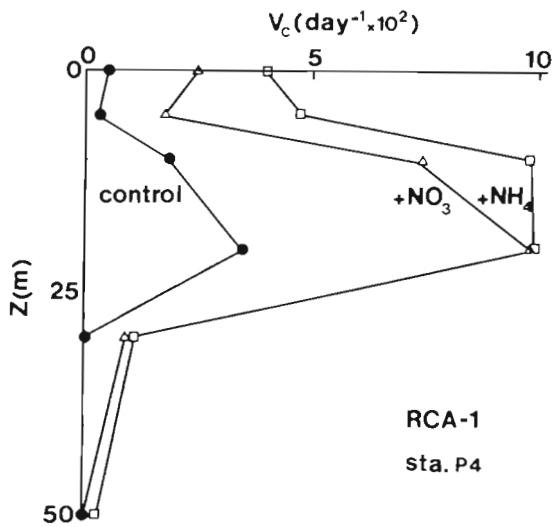

Fig. 4. Effect of ammonium and nitrate on carbon uptake in a euphotic zone profile of coastal waters off Portugal

Nitrogen source experiments

Four stations were sampled in the Equatorial Atlantic, and water samples incubated on deck at surface light with different N sources. N addition always led to a decrease in net C uptake (2- to 3-fold) during the light period (Table 3) for samples initially containing 2.5 µgat NO_3-N l^{-1} (Sta. 129, 130, 134). During the dark period, the effect was not clear-cut, mainly because C uptake rates were barely significant.

Kinetic experiments of N uptake also led to simultaneous decreases in C uptake during the light period (Fig. 5). The greatest decrease in C uptake occurred with small N additions.

Time course experiments

Nitrate enrichments of natural samples generally (6 out of 8 experiments) had no effect on the C uptake during the 10 h incubation periods. Fig. 6A shows a typical example of such a case. The relative precision of the ^{13}C method under field conditions having been established at ± 26 % (Slawyk et al., 1984), the differ-

Table 2. Dissolved inorganic nitrogen (in µgat N l^{-1}) and carbon uptake response ratio (CURR) in euphotic zone profiles

Station	Z (m)	NO_3	NO_2	NH_4	CURR
19	0	2.9	0.09	0.58	0.2
	10	3.0	0.09	0.54	0.7
	20	3.0	0.09	0.52	1.0
	30	2.9	0.09	2.91	1.3
	40	16.8	1.18	0.11	2.0
	50	19.4	0.64	0.07	1.7
	60	19.3	0.09	U	1.3
	75	19.3	0.06	U	–
50	0	3.3	0.09	U	0.4
	20	4.0	0.11	U	0.8
	30	3.8	0.12	0.68	1.4
	40	5.7	0.39	0.82	1.4
	45	14.1	1.14	0.48	1.7
	50	19.0	0.72	U	0.4
	60	19.1	0.72	U	0.5
83	0	U	U	U	0.1
	10	U	0.01	U	0.8
	20	0.3	0.03	U	1.1
	25	4.3	0.15	U	1.1
	30	6.5	0.23	U	5.0
	35	10.5	0.57	U	1.3
	40	11.0	0.58	U	1.0
120	0	U	U	U	0.4
	10	U	U	U	1.7
	20	U	U	U	0.2
	25	0.1	U	U	5.0
	30	5.4	0.18	U	10.0
	35	9.0	0.39	U	2.0
	40	9.9	0.36	U	1.3
	60	11.2	0.06	U	1.7
P4	0	U	U	NA	4.8
	5	U	U	NA	5.7
	10	U	U	NA	4.1
	20	U	U	NA	2.8
	30	0.9	0.14	NA	–
	50	5.9	0.07	NA	–

U: undetectable
NA: not available
CURR values for station P4 were obtained with nitrate additions

Table 3. Evolution of CURR values over several light-dark cycles and as a function of the nitrogen source added

Station 59 N source	First light period	First dark period	Second light period	Second dark period
Nitrate	0.7	4.0	0.7	–
Nitrite	0.9	–	1.1	–
Ammonium	1.4	–	1.5	–
Station 129	Dark period	Light period		
Nitrate	2.0	0.8		
Nitrite	0.8	0.4		
Ammonium	–	0.6		
Urea	1.0	0.4		
Station 130				
Nitrate	–	0.4		
Nitrite	–	0.5		
Ammonium	–	0.3		
Urea	–	0.4		
Station 134				
Nitrate	0.7	0.8		
Nitrite	0.2	0.7		
Ammonium	–	0.5		
Urea	0.7	0.6		

ence between control and experimental samples is not significant in 6 out of 8 such experiments. Fig. 1B also shows the same lack of effect, but in a different way, the isotopic concentrations being presented here.

In 2 out of 8 time courses, 2 kinds of effects occurred that were clearly dependent on the duration of incubation. The most striking example was at Sta. P4-5m, where net C uptake was initially completely stopped during the first 2 h of incubation, and then was stimulated relative to the control (Fig. 6B). This stimulation did not correspond to the exhaustion of the added nitrate. A reduction in net C uptake was also found at Sta. 51 at 20 m upon nitrate addition, with a resulting ten-fold difference between the control and the enriched sample after 10 h of exposure to 10 µgat NO_3-N l^{-1}.

Such changes were also observed in N-limited and N-starved cultures of diatoms (Fig. 7 and 8) with an initial decrease in C uptake, followed by a stimulation. There was, however, considerable variation in those patterns with species (Fig. 9) and cellular nutritional state for a single species (Fig. 7).

For example, C uptake of N-sufficient and N-starved cells of *Phaeodactylum tricornutum* did not respond to N additions, but N-limited cells of the same species exhibited a decrease in C uptake of about 2 orders of magnitude within 2 h of nitrate addition (Fig. 7). This was followed by a slow return to the control value after 6 h of incubation, which corresponded to the exhaustion of the added nitrate. These patterns were reproduced with other N compounds, and inverse relations between C and N uptake were observed during such perturbation experiments (Fig. 8).

The interspecific variability in response of the C uptake system to a nitrate addition is shown in Fig. 9. *Chaetoceros affinis* exhibited a response similar to N-limited cells of *Phaeodactylum tricornutum*, but its C uptake system recovered before nitrate exhaustion (Fig. 9). *Thalassiosira pseudonana* exhibited no

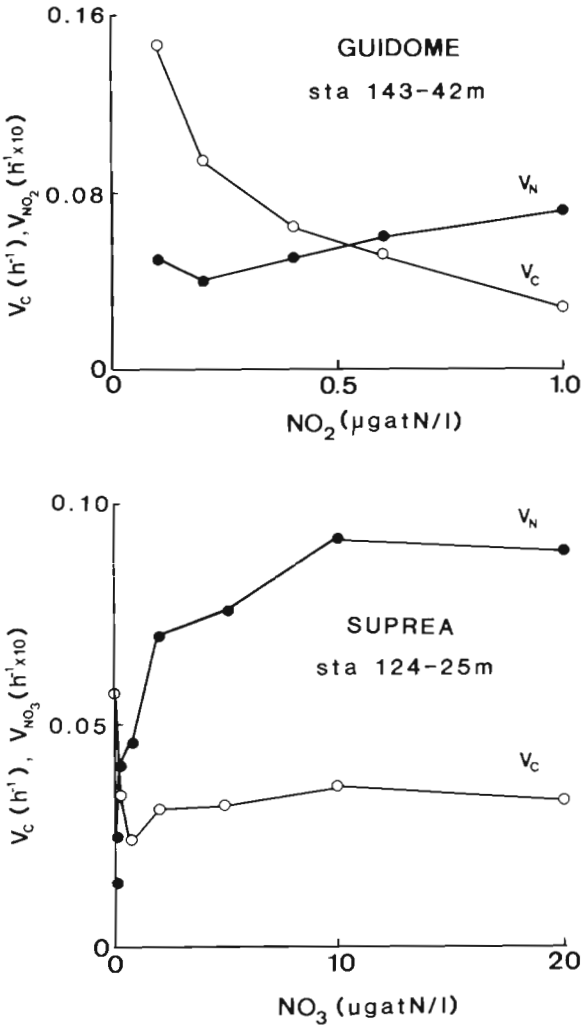

Fig. 5. Influence of nitrogen addition on carbon and nitrogen uptake by natural phytoplankton of tropical and Equatorial Atlantic waters

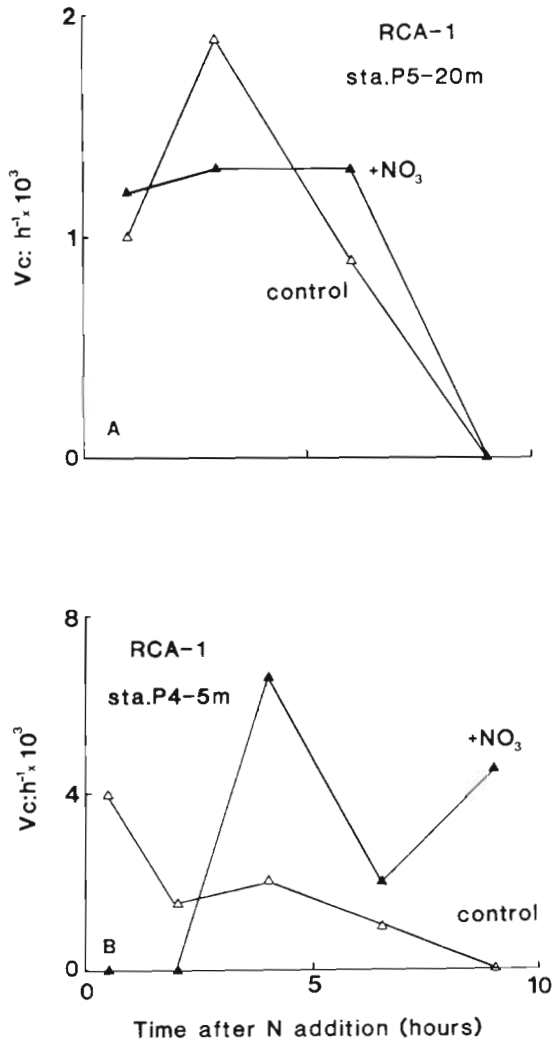

Fig. 6. Time courses of carbon uptake by natural phytoplankton after addition of 10 µgat NO_3-N l^{-1} nutrient depleted waters

response, as to N-starved *P. tricornutum*, although the cells were metabolically active in both cases. Nitrate uptake by *T. pseudonana* was much lower than by the other 2 species (Collos, 1984), so that the added substrate was not exhausted in 24 h, and an eventual stimulation of C uptake could not be observed with the sampling program.

DISCUSSION

Upon addition of inorganic nitrogen to phytoplankton in various nutritional states, we have observed transient changes in net C uptake in euphotic zone profiles, as well as in time series of natural and cultured algal cells. The reductions in C fixation led to inverse relations between C and N uptake, and were sometimes followed by stimulations of carbon uptake.

The influence of inorganic N addition on C uptake

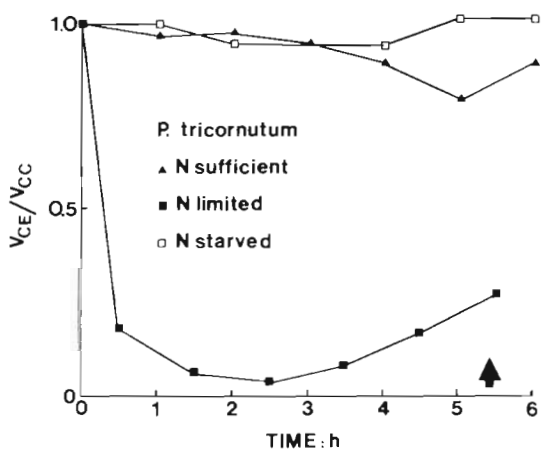

Fig. 7. Time courses of the carbon uptake response ratio (V_{CE}/V_{CC}) after addition of 10 µgat NO_3-N l^{-1} to cells in various nutritional states. Arrow: nitrate exhaustion for nitrogen-limited culture

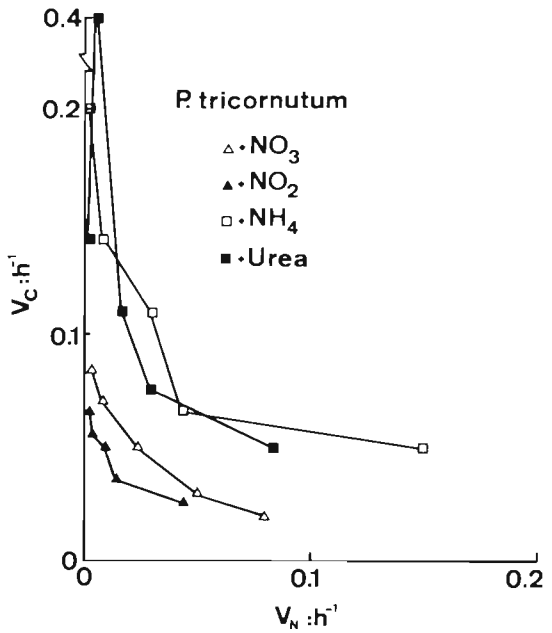

Fig. 8. Relations between carbon and nitrogen uptake by nitrogen-limited cells subjected to nitrogen perturbations once at steady-state

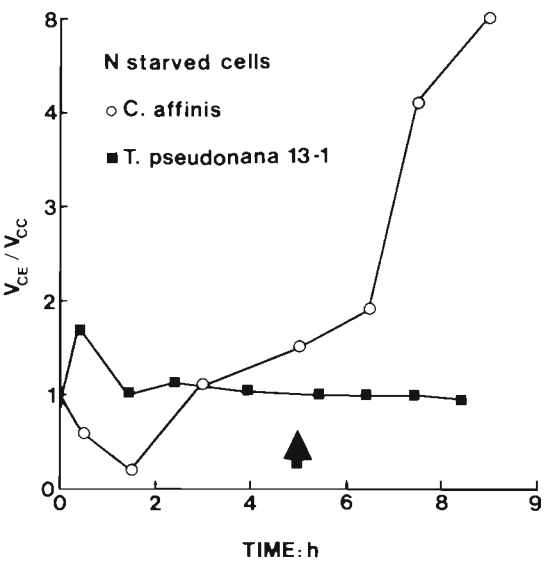

Fig. 9. Time courses of the carbon uptake response ratio (V_{CE}/V_{CC}) after addition of 10 µgat NO_3-N l^{-1} to nitrogen-starved cells of 2 species of diatoms. Arrow: nitrate exhaustion for *Chaetoceros affinis* culture

by phytoplankton is presently the subject of considerable controversy. Some investigators have observed dramatic transient decreases in light C fixation upon N addition to previously N-limited cultures of algal cells (Thomas et al., 1976; Collos and Slawyk, 1979; Terry, 1982; Turpin, 1983) or natural populations of phytoplankton, whose nutritional state, as assessed from ambient nutrient levels, ranged from N-deficient (e.g. MacIsaac and Dugdale, 1972) to N-sufficient (e.g. Falkowski and Stone, 1975). Sometimes, a stimulation of C uptake was noted in the hours following the initial depression (Fedorov and Semin, 1970; Lean and Pick, 1981; Terry and Caperon, 1982; Turpin, 1983). In contrast, others (Morris et al., 1971; Yentsch et al., 1977; MacIsaac et al., 1979; Goldman et al., 1981; Goldman and Dennett, 1983) found no effect at all. Finally, some investigators reported varying responses in different situations (MacIsaac and Dugdale, 1972; Lean et al. 1982).

In view of the remarkable interspecific variability in C uptake to N addition (Fig. 9), conflicting data obtained by different authors on the same species are of particular interest. For example, Morris et al. (1971), Yentsch et al. (1977) and Goldman et al. (1981) did not find any effect of ammonium addition upon light C fixation by *Phaeodactylum tricornutum*, while we did find a reduction (Collos and Slawyk, 1979) and an inverse relation between ammonium and C uptake (Fig. 8) during perturbation experiments. In addition to the possibility of differences in behavior between strains of the same species (Terry et al., 1983), the only major difference between our experimental conditions and theirs appears to be the light level used: 0.014 ly min^{-1} in our study *vs.* 0.050 ly min^{-1} in the other studies (values mentioned in Yentsch et al., 1977 and Goldman and McCarthy, 1978).

The results of Terry (1982) with *Phaeodactylum tricornutum* and *Thalassiosira weissflogii* show that the reduction in net C uptake in samples with added N as compared to controls is greater at lower irradiance levels. Such an effect was also noted by Hattori (1962) who found that C fixation by N-deficient cells of *Anabaena cylindrica* was independent of N additions at high (10,000 lux) but not at low (600 lux) light levels. Although there are other differences between our experimental conditions and those of Goldman et al. (1981) and Yentsch et al.(1977), including temperature and possibly subtle differences in experimental procedures, we suggest that the irradiance level could help explain the discrepancies in results. The same can probably be said of differences between the results of Turpin (1983) and those of Goldman et al. (1981) on *Dunaliella tertiolecta*, the irradiance of 200 µE m^{-2} s^{-1} used in the former study probably being much lower than the 0.06 cal cm^{-2} min^{-1} used in the latter study (470 µE m^{-2} s^{-1} mentioned in Goldman and Dennett, 1983 with apparently the same lighting as in Goldman et al., 1981).

The influence of irradiance on C-N uptake interactions in the field is more difficult to assess. Falkowski and Stone (1975) and Lean and Pick (1981) found that the greatest reduction in C uptake upon N addition occurred at the highest light levels for both ammonium

and nitrate additions, which is in contrast to the results of Hattori (1962) and Terry (1982). Lean et al. (1982) did not report clearcut effects of light on this phenomenon.

Other parameters, such as the N source (Fig. 8) or the N level, can alter the response of the C uptake system. For example, in the study of Lean et al. (1982), a small addition (less than 50 µg $N\,l^{-1}$) led to a stimulation, while a greater additon led to no difference with the control. This may be related to another difficulty coming from the complex N kinetics which are sometimes encountered in the field. For example, in waters where inorganic N (nitrate, nitrite, ammonium) is undetectable, the N uptake kinetics are quite classical (Fig. 5). However, in waters where such nutrients were detectable, a greater substrate addition did not necessarily lead to a greater net N uptake. As in the Eastern Tropical Pacific (MacIsaac and Dugdale, 1972) and the Eastern Equatorial Atlantic (Collos and Slawyk, 1983), we found off Portugal that saturating amounts of $^{15}NO_3$ led to smaller nitrate uptake rates relative to trace additions, near the bottom of the euphotic zone, and particularly where nitrite was present in significant quantities. Such a reduction in the apparent N uptake rates could be due either to an inhibition phenomenon (MacIsaac and Dugdale, 1969; MacIsaac et al., 1974), or to loss of ^{15}N tracer during incubation by a physiological process such as nitrite excretion (Collos and Slawyk, 1983).

Such complex kinetics may be the reason why we did not find an inverse relation between C and N uptake in field samples (except for data shown in Fig. 5) as we found in laboratory cultures (Fig. 8).

The similarity of responses observed with field samples under apparently different environmental conditions does not make their interpretation any easier. For example, net decreases in C uptake were observed in Equatorial Atlantic surface waters (Fig. 3) which were devoid of inorganic N (Sta. 83 and 120), or in which 3 µgat NO_3-$N\,l^{-1}$ were present (Sta. 19 and 50). Although the latter observations are similar to those of Fedorov and Semin (1970), Falkowski and Stone (1975) and Lean et al. (1982), they cannot be explained in terms of nutrient limitation in view of the relatively high nutrient levels encountered simultaneously.

In order to explain those findings by N deficiency, one must invoke that either nutrient conditions change more rapidly than the nutritional state of the phytoplankton, so that N-limited cells can be found in N-rich waters, or that the phytoplankton can perceive small changes in nutrient levels in a range which is generally considered as saturating for the uptake system (about 20 µgat $N\,l^{-1}$ in the studies of Falkowski and Stone, 1975 and Lean et al., 1982). The latter interpretation is appealing in view of the numerous examples showing the capacity of the phytoplankton to change its maximum N uptake rate on a short time scale (Collos, 1983).

One difficulty in interpreting the response of C uptake to N addition in euphotic zone profiles, where time series are not available, comes from its dependence on the incubation time and irradiance level. This limits very seriously the utility of the CURR so far. The variations in the direction of change (decrease or increase) of C uptake upon nutrient perturbations are nevertheless of considerable importance in the sampling strategy of primary production measurements. The first to report such phenomena was probably Becacos (1962) upon phosphate additions to lake water during 6 and 12 h incubations. Since then, others have observed similar patterns in lake (Lean and Pick, 1981) or ocean (Terry and Caperon, 1982) samples. While the relevance of such experimental perturbations to the measurements of primary production in stratified areas depends on advances in knowledge of diffusion and transport processes supplying natural pulses of nutrients to phytoplankton populations, a more immediate application of the present findings concerns bioassays using isotopes (Goldman, 1969), and the possible artefacts in primary production measurements due to the addition of nutrients such as silicate which is present at the millimolar level in isotopic solutions autoclaved in glass ampules (Gieskes and Bennekom, 1973; Slawyk et al., 1984).

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