

Photosynthetic responses of 15 phytoplankton species to ammonium pulsing*

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ABSTRACT: In a series of short-term experiments on marine phytoplankton we found no evidence that transient exposure to high NH_4^+ concentration led to suppression of initial photosynthesis in 13 species previously grown to steady state under NH_4^+ -limitation in continuous culture. Under similar conditions we found up to 60 % initial suppression of photosynthesis in the chlorophyte *Nannochloris* sp. and up to 32 % suppression in the prasinophyte *Platymonas* sp. Recovery followed and was up to 90 % complete by 60 min. These results point toward rather diverse modes of coupling between transient CO_2 fixation and NH_4^+ uptake, but are consistent with our earlier conclusion that rapid NH_4^+ uptake, but relatively undisturbed photosynthesis is the common response of marine phytoplankton exposed to ephemeral patches of NH_4^+ in the pelagic environment.

INTRODUCTION

Rapid ammonium uptake by nitrogen-limited phytoplankton is a well-established phenomenon (Conway and Harrison, 1977; McCarthy and Goldman, 1979; Goldman and Glibert, 1982). It is not so clear, however, as to how photosynthesis is coupled to NH_4^+ uptake under these conditions. For example, in our previous studies we preconditioned 4 marine phytoplankton species (*Phaeodactylum tricoratum* [TFX-1], *Thalassiosira weissflogii* [Actin], *Chaetoceros simplex* [Bbsm], *Dunaliella tertiolecta* [Dun]) to different degrees of NH_4^+ limitation under continuous cultivation and then pulsed them with saturation levels of NH_4^+ . Although NH_4^+ uptake generally was significantly greater than required for balanced growth during the first minutes of incubation (Goldman and Glibert, 1982), we could find no evidence for either stimulation or suppression of photosynthesis for up to hours of incubation (Goldman et al., 1981; Goldman and Dennett, 1983). Turpin (1983), in contrast, tested *D. tertiolecta*, under conditions virtually identical to ours and found that the initial photosynthetic rate was significantly suppressed in cultures that were strongly

nitrogen-limited. Recovery was a function both of the concentration of pulsed NH_4^+ and the duration of incubation.

In an attempt to resolve whether or not these grossly different results were caused by methodological or species-specific differences, we supplied Dr. Turpin with our culture of *Dunaliella tertiolecta* (clone Dun) which we had obtained from the culture collection of Dr. R. R. L. Guillard. Turpin's culture of *D. tertiolecta*, obtained from the Northeast Pacific Culture Collection, Department of Oceanography, University of British Columbia and designated NEPCC-1, was presumed to be the Dun clone, since it originally was obtained from the WHOI culture collection (Turpin, 1983).

In addition, we expanded our studies on NH_4^+ pulsing to include 11 more species (9 marine and 2 freshwater) besides the 4 marine species we tested earlier. In reviewing the literature on NH_4^+ pulsing it was clear that, exclusive of our own studies, not only have a limited number of additional species been tested for their photosynthetic response to NH_4^+ pulsing under conditions of nitrogen limitation, but the results have been somewhat variable (e. g. Fogg, 1956; Kanazawa et al., 1970; Lawrie et al., 1976; Thomas et al., 1976; Collos and Slawyk, 1979; Healey, 1979; Turpin, 1983). We thus suspected that the differing results among

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experimentalists might have been due as much to species-specific differences as to any other factor.

MATERIALS AND METHODS

We grew 15 phytoplankton species to steady state in NH_4^+ -limited continuous cultures exactly as described before (Goldman et al., 1981; Goldman and Dennett, 1983). Thirteen species were marine, including 5 diatoms – *Thalassiosira weissflogii* (Actin), *Phaeodactylum tricorutum* (TFX-1), *Chaetoceros simplex* (Bbsm), *Thalassiosira pseudonana* (3-H), and *Thalassiosira pseudonana* (13-1); 3 chrysophytes – *Pavlova lutheri* (Mono), *Isochrysis galbana* (T. Iso), and *Olisthodiscus luteus* (Olisth); 1 cryptophyte – *Chroomonas salina* (3-C); 1 prasinophyte – *Platymonas* sp. (Platy I); and 3 chlorophytes – *Dunaliella tertiolecta* (Dun), *Nannochloris* sp. (GSB Nanno), and *Chlorella capsulata* (Fla E). Two species were freshwater chlorophytes – *Selenastrum capricornutum* and *Scenedesmus obliquus*. All the marine species were obtained from the culture collection of R. R. L. Guillard, except *I. galbana* (T. Iso), which we obtained from S. Gallager at the Environmental Systems Laboratory at WHOI. *S. capricornutum* came from the US Environmental Protection Agency in Corvallis, Oregon and *S. obliquus* came from the laboratory of M. Gibbs at Brandeis University.

We grew cultures to steady state at relatively low dilution rates (= specific growth rate μ) in either an artificial seawater (Goldman and McCarthy, 1978) or freshwater medium (Goldman and Graham, 1981) that contained $100 \mu\text{g atoms l}^{-1}$ of NH_4^+ and $10 \mu\text{g atoms l}^{-1}$ of PO_4^{3-} to insure nitrogen limitation. Dilution rates were varied between ca 0.3 and 0.5 d^{-1} so that the ratio $\mu : \hat{\mu}$ (where $\hat{\mu}$ = maximum specific growth rate) always was less than 0.5 , which, according to Turpin (1983), is the relative growth rate below which suppression of photosynthesis approaches maximal levels after NH_4^+ enrichment. Cultures were maintained at steady state and tested for short-term photosynthetic response in the presence of added NH_4^+ at the same temperature and light intensity. Light intensities were held constant at ca $470 \mu\text{E m}^{-2} \text{ s}^{-1}$ but several temperatures were used: 16°C for *Dunaliella tertiolecta*, *Phaeodactylum tricorutum*, *Chaetoceros simplex*, and *Thalassiosira weissflogii*, 25°C for *Nannochloris* sp., and 20°C for the remaining species. Light intensities were measured with a Biospherical Instruments QSL-100 4π sensor and quantum scalar irradiance meter.

Once steady state conditions were attained, we withdrew samples and divided them into 2 portions. The first portion was used for analyses of particulate carbon, particulate nitrogen, residual NH_4^+ , and dissolved inorganic carbon (DIC). Particulate carbon and

particulate nitrogen were measured with a Perkin Elmer 240 elemental analyzer on samples retained on pre-combusted glass fiber (Whatman GF/F) filters and NH_4^+ was measured on the filtrate immediately after collection (McCarthy and Kamykowski, 1972). DIC was measured on refrigerated samples with a Dohmann PR-1 carbon analyzer.

The second portion was used in a series of time-course experiments to measure short-term CO_2 fixation in the absence and presence of NH_4^+ enrichment. The protocols for these experiments were identical to those used previously (Li and Goldman, 1981; Goldman et al., 1981; Goldman and Dennett, 1983). Incubation chambers were 150 ml water-jacketed reaction vessels. Chamber contents were continuously mixed by magnetic bar stirring.

We first added $0.5 \mu\text{Ci } \mu\text{mol DIC}^{-1}$ of $\text{H}^{14}\text{CO}_3^-$ and $16 \mu\text{g atoms l}^{-1}$ of NH_4^+ to one incubation chamber and only ^{14}C to a replicate chamber. The added NH_4^+ was sufficient to saturate uptake (Goldman and Glibert, 1983). The experiment was started by addition of 25 ml of culture to each chamber. Whole culture aliquots (1 ml) were withdrawn in approximate 10 min intervals over a 60 min incubation period for most of the experiments. Additional repeat measurements were made in a few experiments on the 4 species we tested previously (Goldman et al., 1981): 15 min single end-point measurements on *Phaeodactylum tricorutum*, *Chaetoceros simplex*, and *Thalassiosira weissflogii* and both 15 min single end-point and 90 min time-course measurements on *Dunaliella tertiolecta*. Samples were placed directly in glass scintillation vials containing 2 ml methanol acidified with 5 % glacial acetic acid. The vial contents were evaporated to dryness under an infrared lamp, resuspended in 1 ml distilled water, followed by 10 ml scintillation fluid (Scintiverse II). Radioactivity was measured directly by liquid scintillation counting on a Beckman LS-100C spectrometer.

The specific carbon rates $\mu'(-)$ (without NH_4^+ enrichment) and $\mu'(+)$ (with NH_4^+ enrichment) were determined from the relation $\bar{a} \Delta t^{-1} \ln[(\text{PC} + \Delta^{14}\text{C}) \text{PC}^{-1}]$, where $\Delta^{14}\text{C}$ = amount of labelled carbon incorporated over the period Δt ; PC = particulate carbon concentration at the start of the incubation; \bar{a} = a correction factor to account for isotopic discrimination (taken to be 1.05). Except where noted, μ' was determined from the slope of the time-course curves.

The impact of NH_4^+ enrichment on photosynthesis was calculated in 2 ways: either as a comparison of $\mu'(+)$ with $\mu'(-)$ or from the expression $A_t = {}^{14}\text{C}(+) : {}^{14}\text{C}(-)$ in which A_t is the accumulation factor after t min incubation and ${}^{14}\text{C}(+)$ and ${}^{14}\text{C}(-)$ are, respectively, the total accumulated ^{14}C after t min in the presence and absence of added NH_4^+ . Values of $A_t > 1$ indicate

stimulation of ^{14}C uptake, values < 1 indicate suppression, and values $= 1$ represent no effect.

RESULTS

NH_4^+ limitation was assured in virtually all experiments. Residual NH_4^+ concentrations were always undetectable ($< 0.03 \mu\text{g atoms l}^{-1}$) and particulate C:N ratios were, with one exception (*Chroomonas salina*), > 9 (Table 1).

We could find no evidence for significant photosynthetic suppression in 13 of the 15 species we tested (Table 1; Fig. 1 and 2). There did appear to be some slight time-dependent increases (Fig. 1 B) or decreases in A_t (Fig. 2 E). Although slight suppression or stimulation of photosynthesis in these studies cannot be ruled out, we suspect that such small variations are as much due to inherent limitations of the assay as they are to

any real physiological effect. In none of the time-course experiments was the initial value of A_t (A_{10}) below 0.84, and in fact, most values of A_{10} were close to, or slightly greater than 1 (Table 1). Moreover, there were no substantial changes in A_t during the course of these incubations, although in some cases where experiments were replicated the average values of A_t varied by up to about 0.1 (Fig. 1 A and 1 E). The single end-point measurement of A_{15} in the diatom *Thalassiosira weissflogii* (Actin) was 0.81 (Table 1), but in numerous earlier studies with this species (as well as with *Dunaliella tertiolecta*, *Phaeodactylum tricornutum*, and *Chaetoceros simplex*) we found no evidence of even slight photosynthetic suppression after NH_4^+ pulsing (see Fig. 1 and 2 in Goldman et al., 1981).

In stark contrast, we found a dramatic reduction in A_{10} to < 0.49 in 4 replicate experiments with *Nannochloris* sp. (Table 1). This initial suppression of photosynthesis

Table 1. Steady state growth characteristics of 15 phytoplankton species precultured in NH_4^+ -limited continuous cultures and short-term photosynthetic response after enrichment with saturating NH_4^+

Species	D (d^{-1})	C:N ratio (wt:wt)	A_t^*
Diatoms			
<i>Thalassiosira pseudonana</i> (3H)	0.29	9.3	1.08
	0.48	9.3	1.03
<i>Thalassiosira pseudonana</i> (13-1)	0.50	13.0	0.92
<i>Phaeodactylum tricornutum</i> (TFX-1)	0.37	10.2	0.87**
<i>Chaetoceros simplex</i> (Bbsm)	0.37	13.4	0.98**
<i>Thalassiosira weissflogii</i> (Actin)	0.37	14.9	0.81**
Chrysophytes			
<i>Pavlova lutheri</i> (Mono)	0.48	9.8	1.09
<i>Olisthodiscus luteus</i> (Olisth)	0.51	14.2	0.94
	0.53	11.7	0.96
<i>Isochrysis galbana</i> (T. Iso)	0.48	8.8	0.99
	0.49	10.1	0.84
Cryptophyte			
<i>Chroomonas salina</i> (3-C)	0.29	7.1	1.13
	0.48	5.9	1.20
Chlorophytes			
<i>Dunaliella tertiolecta</i> (Dun)	0.36	14.7	1.09**
	0.35	13.3	1.11**
	0.67	10.6	1.22**
<i>Chlorella capsulata</i> (Fla E)	0.48	10.5	0.85
<i>Selenastrum capricornutum</i>	0.30	12.4	0.86
<i>Scenedesmus obliquus</i>	0.30	11.2	0.93
<i>Nannochloris</i> sp. (GSB Nanno)	0.29	19.2	0.49
	0.30	18.1	0.41
	0.35	16.4	0.48
	0.52	11.8	0.41
Prasinophyte			
<i>Platymonas</i> sp. (Platy I)	0.29	25.5	0.83
	0.30	26.7	0.77
	0.49	27.0	0.68

* 10 min accumulation factor, except where indicated
 ** 15 min accumulation factor

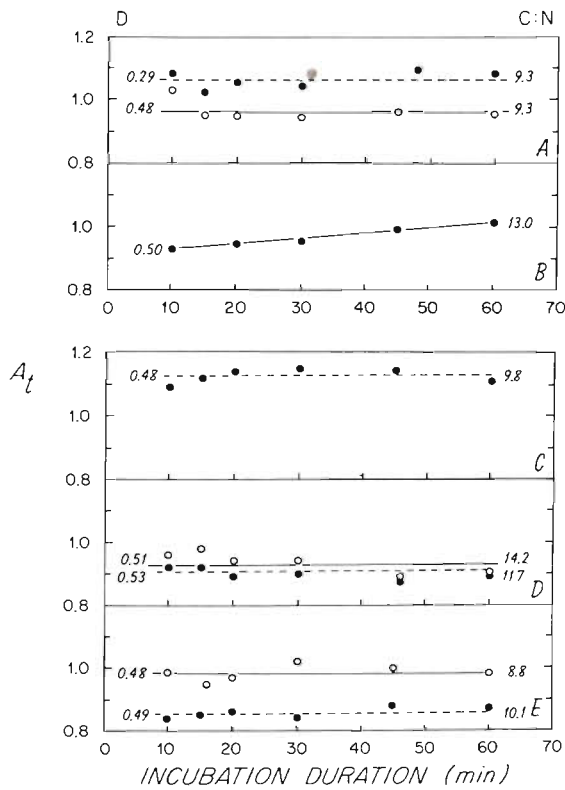


Fig. 1. Effect of NH_4^+ pulsing on the accumulation factor A_t over time in phytoplankton species precultured to stated dilution rate D and steady state $C:N$ ratio in continuous culture. Different symbols represent replicate experiments (A) *Thalassiosira pseudonana* (3H); (B) *Thalassiosira pseudonana* (13-1); (C) *Pavlova lutheri* (Mono); (D) *Olithodiscus luteus* (Olish); (E) *Isochrysis galbana* (T. Iso)

was followed by recovery until A_{60} was greater than 0.80 (Fig. 3 B). We observed a similar, but less dramatic trend in the time course data from 3 replicate studies with *Platymonas* sp. (Fig. 3 A) – an increase from $A_{10} = 0.68$ to 0.83 to $A_{60} > 0.90$. The time-dependency of recovery thus was the major criterion we used to determine whether or not there was significant initial suppression of photosynthesis.

We summarized all the data from our current and previous (Goldman et al., 1981; Goldman and Dennett, 1983) experiments in a plot of $\mu'(+) \text{ versus } \mu'(-)$ (Fig. 4). With the exception of the 2 species we identified as being sensitive to NH_4^+ pulsing, all the combined data fell within or close to $\pm 10\%$ of the line representing a non-effect, i.e. $\mu'(+) = \mu'(-)$.

DISCUSSION

The apparent discrepancy between our earlier results (Goldman et al., 1981) and those of Turpin (1983) seems to be resolved. Elrifi and Turpin (1985)

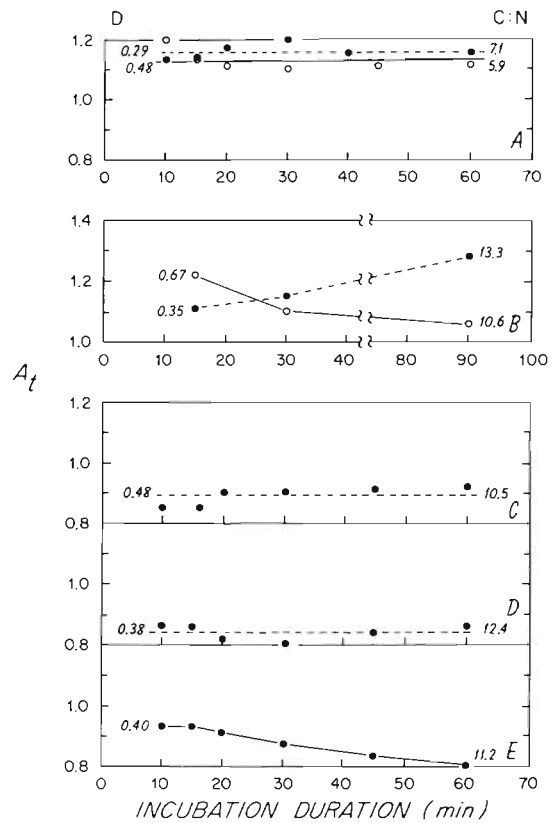


Fig. 2. Same as Fig. 1. (A) *Chroomonas salina* (3-C); (B) *Dunaliella tertiolecta* (Dun); (C) *Chlorella capsulata* (Fla E); (D) *Selenastrum capricornutum*; (E) *Scenedesmus obliquus*

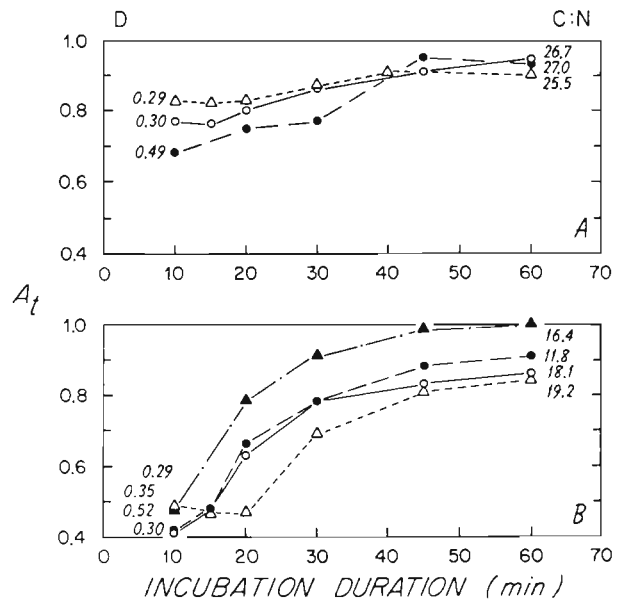


Fig. 3. Same as Fig. 1. (A) *Platymonas* sp. (Platy I); (B) *Nannochloris* sp. (GSB Nanno)

compared our clone of *Dunaliella tertiolecta* (Dun) with their NEPCC-1 clone under conditions identical to ours and, like us, found no evidence for NH_4^+ -

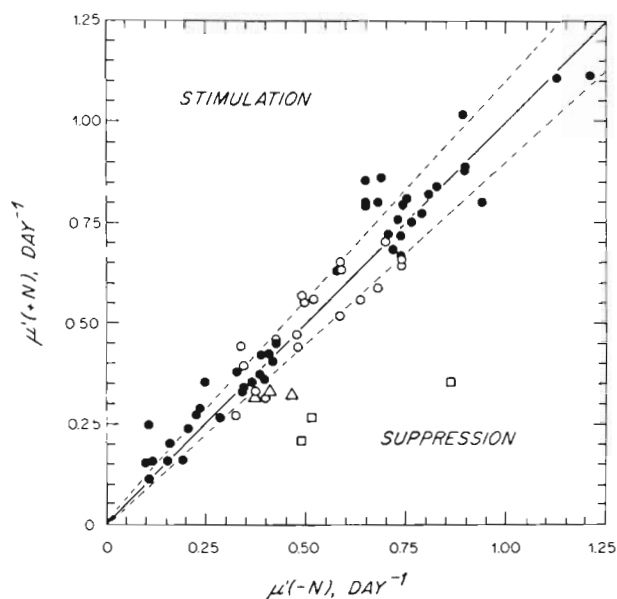


Fig. 4. Summary plot of specific carbon uptake rate μ' (+) versus μ' (-) for current and earlier experiments. For clarity all previous data for *Dunaliella tertiolecta* (Dun), *Thalassiosira weissflogii* (Actin), *Phaeodactylum tricorutum* (TFX-1), and *Chaetoceros simplex* (Bbsm) from Goldman et al. (1981) and Goldman and Dennett (1983) are represented by a common closed symbol (●). All current data are represented by open symbols: *Platymonas* sp. (□), *Nannochloris* sp. (Δ), all other data (○). Solid line represents theoretical one to one relation between μ' (+) and μ' (-), dashed lines represent $\pm 10\%$ of theoretical relation

induced suppression of photosynthesis in the Dun clone; severe suppression was, however, evident once again in the NEPCC-1 clone. It seems highly likely, therefore, that the NEPCC-1 clone of *D. tertiolecta* from the Northeast Pacific Culture Collection is not the Dun clone, as previously thought (Turpin, 1983). These results, together with our current finding that photosynthesis in at least 2 marine species is inhibited for short periods by NH_4^+ pulsing, point toward rather diverse modes of coupling between CO_2 fixation and NH_4^+ uptake in, not only different species, but clones of the same species as well.

The pattern of initial suppression we observed, followed by rapid recovery (Fig. 3) is identical to what Turpin (1983) observed in his study on the NEPCC-1 clone of *Dunaliella tertiolecta* and to what Healey (1979) found with the freshwater chlorophyte *Scenedesmus quadricauda*. Although we did not measure NH_4^+ depletion over time, we suspect that the time-course of recovery of photosynthesis was correlated to some degree with the disappearance of NH_4^+ from solution, as was shown by Turpin (1983). However, in an earlier study on rapid NH_4^+ uptake (Goldman and Glibert, 1982) depletion of $16 \mu\text{g atoms l}^{-1}$ added NH_4^+ by several species capable of very rapid

initial NH_4^+ uptake under conditions identical to those in the current study generally took far longer than 60 min. Thus the almost full recovery in photosynthesis by 60 min in the 2 susceptible species is not easily explained.

Healey (1979) suggested that competition for ATP and reducing electrons between CO_2 and NH_4^+ during the initial period of rapid NH_4^+ uptake might be the cause of the initial but short-lived suppression. Turpin (1983) questioned this interpretation because, as shown by Syrett (1958) and Ohmori and Hattori (1978), recovery of initial losses of ATP during NH_4^+ pulsing occurs well before depletion of added NH_4^+ . Another possible explanation for this species-specific phenomenon is that cytoplasmic NH_3 can be very toxic and, unless assimilated and metabolized very rapidly, could lead to initial inhibition of photosynthesis (Bassham, pers. comm.). NH_4^+ concentrations per cell volume are known to reach molar concentrations (Wheeler, 1983) and most likely are even higher in individual cellular compartments. Thus even though cytoplasmic pH may be no higher than external pH (ca 8), sufficient cytoplasmic NH_3 could be produced to cause significant reductions in photosynthesis. Species-specific differences in the rates and mechanisms by which NH_4^+ is transported across the cell membrane, stored within the cytoplasm (or vacuoles), and finally assimilated into amino acids may thus be important factors governing how CO_2 fixation is coupled to rapid removal of exogenous NH_4^+ .

In trying to gauge the ecological significance of this form of transient behavior in phytoplankton it is extremely important to distinguish between NH_4^+ and NO_3^- as substrates that might compete with CO_2 for available energy in the light. Most likely, NO_3^- addition has a profoundly different effect on the photosynthetic apparatus than does NH_4^+ enrichment, particularly since it is well-established that competition between NO_3^- and CO_2 for reducing electrons occurs when cells are suddenly exposed to high NO_3^- levels (Syrett, 1981) and that NO_3^- uptake and assimilation require substantially more energy than needed for equivalent NH_4^+ processes. Certainly, the evidence for NO_3^- suppression of photosynthesis among a diverse group of phytoplankton species is compelling (Thomas et al., 1976; Collos and Slawyk, 1979; Terry, 1982; Hipkin et al., 1983; Elrifi and Turpin, 1985), although exceptions have been noted, e.g. the freshwater chlorophyte *Ankistrdesmus braunii* (Elrifi and Turpin, 1985) and the marine diatom *Chaetoceros simplex* (Goldman and Dennett, 1983).

Our interest has been focused primarily on the ways in which transient NH_4^+ uptake affects photosynthesis since recycled NH_4^+ is the major nitrogen source found in pelagic surface waters. Thus, there is no

disagreement that NH_4^+ -induced suppression of short-term photosynthesis has been found in several phytoplankton species – interestingly, all chlorophytes or related species (Thomas et al., 1976; Healey, 1979; Turpin, 1983; Elrifi and Turpin, 1985). Our own evidence that only 1 chlorophyte, *Nannochloris* sp., and a closely related prasinophyte, *Platymonas* sp., out of a diverse group of 15 phytoplankton species we examined, were sensitive to NH_4^+ pulsing, however, leads us to reconfirm our earlier conclusion (Goldman et al., 1981) that rapid NH_4^+ uptake, but relatively undisturbed CO_2 fixation, is the common response of marine phytoplankton exposed to ephemeral patches of NH_4^+ in the pelagic environment.

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