Effects of the light regime on nutrient assimilation by phytoplankton in the Baja California and northwest Africa upwelling systems

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ABSTRACT

The ability of natural phytoplankton assemblages in the Baja California and northwest Africa upwelling regions to assimilate nitrate, ammonium and silicic acid at simulated in situ light intensity and in the dark, was determined in 6 hr tracer experiments using the stable isotopes ^{15}N and ^{30}Si. Nitrate was almost never taken up in the dark, but dark uptake rates of ammonium and silicic acid ranged from zero to values equal to those measured at saturating light intensity. The capacity for dark uptake of silicic acid showed systematic variability, with the mean ratio of dark to light uptake (V_{DK}/V_{LT}) significantly lower off northwest Africa than off Baja California and, within the Baja California system, lower during thermally stratified periods than during upwelling periods. Variability in V_{DK}/V_{LT} for ammonium was not clearly associated in time with hydrographic phenomena, and no systematic differences between the dark ammonium uptake capacities of Baja California and northwest Africa phytoplankton could be detected. Comparison of these results with those of nutrient uptake kinetic studies performed on the same cruises indicates that the light regime was substantially more important than the nutrient concentration regime in controlling the biological availability of dissolved nitrogen and silicon in these two upwelling systems.

1. Introduction

In the upwelling regions located off the west coasts of major land masses the near-surface concentrations of nitrate, phosphate and silicic acid are generally high enough that nutrient uptake and growth rates of the phytoplankton are not substrate-limited (MacIsaac and Dugdale, 1969; Dugdale and Goering, 1970; Goering *et al.*, 1973; Nelson, 1975; Hulburt, 1976; Nelson and Goering, 1978). Additionally, such regions are typified by strong equatorward winds (Wooster and Reid, 1963; Cushing, 1971) and exhibit high chlorophyll concentrations and light extinction coefficients (Ryther *et al.*, 1970; Barber and Huntsman, 1974, 1975). The combined effect of

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strong winds and pronounced light extinction is often to mix surface water and its associated phytoplankton populations to depths where little light penetrates. Thus, high nutrient concentrations, deep wind mixing and rapid light extinction combine to make the potential role of the light regime in controlling rates of algal processes greater in upwelling regions than in other parts of the near-surface ocean.

Nutrient assimilation by marine phytoplankton is ultimately dependent upon light as an energy source, as is all plant metabolism. The biochemical mechanisms by which such light dependence is imposed are presently not well understood. However, evidence is accumulating rapidly to suggest that coupling between photosynthetic energy fixation and nutrient uptake may differ among the major nutrients in ecologically significant ways. MacIsaac and Dugdale (1972) developed a hyperbolic model to fit their experimental data showing light dependence of nitrate and ammonium uptake in natural phytoplankton populations in the eastern Mediterranean, the eastern tropical Pacific and the upwelling region off Peru. They showed that the dependence of the specific uptake rate, V, upon the ambient light intensity, I, could be described by a rectangular hyperbola, and proposed a kinetic equation similar to Dugdale's (1967) equation relating the uptake rate of a limiting nutrient to its concentration in the external medium:

$$V = V_{\max} \frac{I}{K_I + I} \tag{1}$$

where $V_{\max}$ is the specific uptake rate at saturating light intensity and K_I the light intensity at which $V = V_{\max}/2$. Equation (1) implies that light can be treated mathematically as a necessary substrate for nutrient uptake in exactly the same manner as the nutrient itself, and notably demands that $V = 0$ in the dark. Falkowski and Stone (1975) showed that ATP used in nitrate uptake is produced mainly via cyclic photophosphorylation in the presence of light, thus providing a biochemical mechanism for strong light dependence of nitrate uptake. Uptake of inorganic nitrogen in the dark has been observed in the diatom *Ditylum brightwellii* (Eppley and Coatsworth, 1968), the coccolithophore *Coccolithus huxleyi* (Eppley *et al.*, 1971), and the tropical oceanic dinoflagellates *Pyrocystis noctiluca* and *Dissodinium lunula* (Bhovichitra and Swift, 1977), but field studies reported to date have indicated little dark uptake of nitrate or ammonium by natural phytoplankton assemblages (Dugdale and Goering, 1967; MacIsaac and Dugdale, 1972).

Davis (1973) extended the strong light dependence concept to silicic acid uptake, and showed that equation (1) provided a good fit to his data on light dependence of silicic acid uptake by *Skeletonema costatum* during 5-7 day perturbation experiments in continuous culture. However, silicic acid uptake appears to differ from nitrate and ammonium uptake in that there have been numerous observations of light dependence much weaker than that implied by equation (1), both in unialgal diatom cultures and in the ocean. Goering *et al.* (1973) showed that silicic acid uptake by a

natural phytoplankton population in the Peru upwelling system continued at a substantial rate throughout the night, while nitrate and ammonium uptake did not. Azam and Chisholm (1976) observed a pronounced silicic acid uptake maximum around midnight in the Gulf of California. Vertical profiles of ^{14}C, ^{15}N and ^{30}Si assimilation rates in the Baja California and northwest Africa upwelling regions indicate that silicic acid uptake proceeded at a significant rate at depths receiving less than 1% of the surface light intensity, where nitrate and ammonium uptake rates were substantially reduced and photosynthesis negligible (Nelson and Goering, 1978). Nelson *et al.* (1976) found that silicic acid uptake in unialgal cultures of the marine diatom *Thalassiosira pseudonana* proceeded in the dark at the same rate as in full light for at least 4 hr when cultures were grown at saturating light intensity prior to the experiment. They suggested that because silicic acid uptake is an energy-requiring process closely linked to aerobic respiration and ATP production (Lewin, 1955), a transition from high to low capacity for dark uptake may take place with time in the dark, due to depletion of the cells' stored energetic reserves.

The present paper reports a study of the degree to which light is required for uptake of nitrate, ammonium and silicic acid by natural phytoplankton in two coastal upwelling regions. This study was conducted during I.D.O.E. Coastal Upwelling Ecosystems Analysis program cruises to Baja California in 1973 (MESCAL II) and northwest Africa in 1974 (JOINT I). Other features of nutrient uptake in these two systems, and specifically the lack of nutrient limitation, have been reported elsewhere (Whitledge and Conway, 1977; Nelson and Goering, 1978; Conway and Harmon, unpublished). The study reported here thus tested the hypothesis that the light regime often controls nutrient uptake by phytoplankton in nutrient-rich regions of the ocean, and that the differing responses of three nutrient uptake mechanisms to light cause this control to be different for each of the three nutrients in natural systems.

2. Methods

At 29 stations off the Baja California coast, and 24 off the northwest Africa coast, seawater was collected in 30-liter Niskin bottles from the depth to which 50% of the incident surface light penetrated, as calculated from Secchi disc readings (Baja California) or determined with a submersible quantum meter (northwest Africa). Station locations are presented in Figure 1. The 50% light penetration depth was typically located at ca. 3 m in both regions, and ranged from 1.5 to 5.5 m depending upon turbidity. This depth was selected for light experiments because it frequently represents the depth of maximum photosynthetic activity in upwelling regions (e.g. Strickland *et al.*, 1969; Ryther *et al.*, 1970), and ^{14}C studies conducted concurrently with experiments reported here indicate that this was also the case in the Baja California and northwest Africa systems (Barber and Huntsman, 1974, 1975).

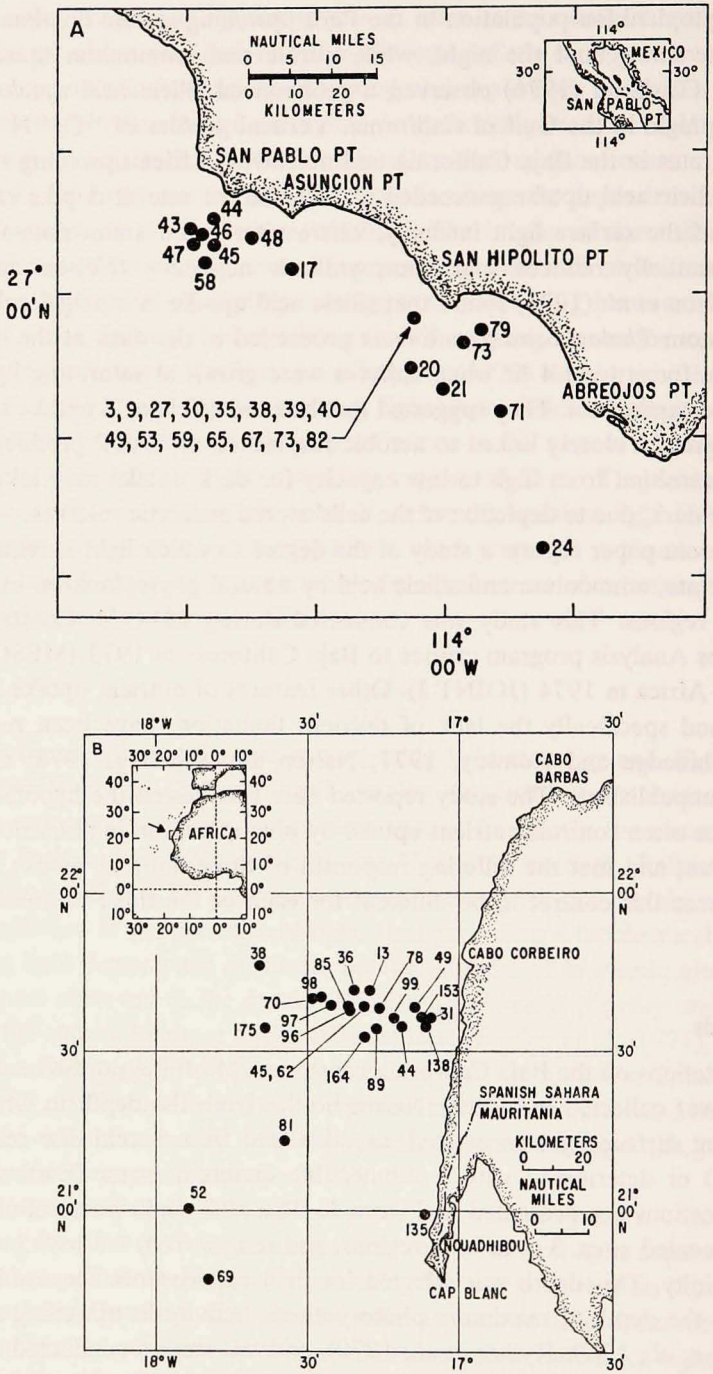

Figure 1. Locations of stations where light dependence experiments were performed. a) Baja California; b) northwest Africa.

Seawater was drawn into pairs of 2-liter glass serum bottles for nitrate or ammonium uptake rate measurements, or 2.3-liter Plexiglas bottles for silicic acid uptake rate measurements. One bottle of each pair was fitted with a neutral density metal screen (Perforated Products, Inc. #15G) that transmitted 50% of the incident light, and the other darkened with black epoxy paint and black electrical tape applied to the outside surface. Samples were inoculated with 1.0 ml of $^{15}NH_4Cl$ (20.0 μg atoms N • ml^{-1}; 99 atom % ^{15}N), Na $^{15}NO_3$ (20.0 μg atoms N • ml^{-1}; 95 atom % ^{15}N), or H_4 $^{30}SiO_4$ (20.0 μg atoms • ml^{-1}; 95.6 atom % ^{30}Si) solutions, respectively, and incubated on deck for 6 daylight hours in Plexiglas incubation chests maintained at sea surface temperature by continuous flow of surface seawater. Details of the procedures employed in ^{15}N analysis and uptake rate calculations are given by Pavlou *et al.* (1974) and ^{30}Si analytical procedures are described by Nelson and Goering (1977). Stable isotope tracer experiments yield element-specific uptake rates (V) in units of moles N (or Si) taken up per mole particulate N (or Si) initially present per hour, which reduces dimensionally to (hr^{-1}) (Sheppard, 1962). The ratio of the specific uptake rate in the dark bottle (V_{DK}) to that in the bottle incubated at simulated in situ light intensity (V_{LT}) was computed for each sample pair as a measure of the degree to which the uptake rate was independent of ambient light.

More detailed light dependence experiments were performed at the stations indicated in Table 1. At these stations water was collected from depths ranging from the surface to the 0.1% light penetration depth, and drawn into series of incubation bottles fitted with neutral density metal screens or darkened with black electrical tape and epoxy paint to provide light transmissions ranging from 100% to 0. Samples were inoculated, incubated and analyzed isotopically as described above. The specific uptake rate (V) was plotted as a function of light intensity (I), and in those experiments where the dependence of V upon I appeared to be describable by hyperbolic saturation kinetics the parameters V_{max} and K_I (MacIsaac and Dugdale, 1972) were calculated by a least-squares fit to equation (1) (Cleland, 1967).

At 4 stations on MESCAL II (27, 30, 58 and 59) and 5 on JOINT I (13, 30, 38, 70 and 78) seawater was collected at 5-6 depths ranging from the surface to that of 1% surface light penetration. Samples were inoculated with $^{15}NH_4^+$, $^{15}NO_3^-$ or $H_4{}^{30}SiO_4$. One half of each sample was incubated at a light intensity simulating that at the depth from which the sample was collected (using neutral density metal light screens) and the other half in the dark. Incubation conditions and subsequent sample preparation and analysis were as described above. These experiments provided vertical profiles of the substrate-saturated nutrient assimilation rates at simulated in situ light intensity, and of the maximum uptake rates that could be sustained in the absence of photosynthesis, at the stations sampled.

3. Results

All comparisons between light and dark uptake rates of nitrate, ammonium and

Table 1. Stations and depths at which seawater was collected for nutrient uptake rate vs. light intensity experiments.

Baja California

Station	Depth (4)	Depth (% surface light)	Substrates
9	0	100	NO_3^-, H_4SiO_4
9	2.5	50	NO_3^-, H_4SiO_4
9	7.0	25	NO_3^-, H_4SiO_4
9	12	10	NO_3^-, H_4SiO_4
9	23	1	NO_3^-, H_4SiO_4
35	3.0	50	H_4SiO_4
71	3.0	50	H_4SiO_4
82	5.0	50	H_4SiO_4
82	16	10	H_4SiO_4

Northwest Africa

Station	Depth (4)	Depth (% surface light)	Substrates
6	3.0	50	H_4SiO_4
31	2.2	50	H_4SiO_4
38	2.0	50	H_4SiO_4
52	2.6	50	NH_4^+, NO_3^-
52	55	0.01	NH_4^+
62	3.0	50	NH_4^+, H_4SiO_4
62	60	0.1	NH_4^+, H_4SiO_4
69	2.0	50	NH_4^+, H_4SiO_4
69	55	0.1	NH_4^+, H_4SiO_4
85	2.0	50	NH_4^+, NO_3^-
85	33	0.1	NH_4^+, NO_3^-
135	2.0	50	H_4SiO_4

silicic acid in water collected from the 50% light penetration depth are presented in Tables 2 and 3. The ratio of dark to light uptake varied from 0 to >1 for ammonium and silicic acid, but not nitrate. Substantial rates of nitrate uptake in the dark, although observed at MESCAL II stations 24 and 39, were rare. The analytical precision of ^{15}N and ^{30}Si uptake rate measurements is ca. ±10% (Dugdale and Goering, 1967; Nelson and Goering, 1977), so an analytically detectable effect of light is present in those comparisons where V_{DK}/V_{LT} differs from unity by more than 0.10. By this criterion, inhibition of uptake by light (V_{DK}/V_{LT} >1.10) was never observed for nitrate or silicic acid, but ammonium uptake may have been light-inhibited at one station (MESCAL II station 78; $V_{DK}/V_{LT} = 1.46$).

Table 2. The specific uptake rate at simulated in situ light intensity (V_{LT}) and in the dark (V_{DK}) of nitrate, ammonium and silicic acid, and the ratio of dark to light uptake (V_{DK}/V_{LT}) in seawater collected from the 50% light penetration depth at 29 stations in the upwelling region off Baja California in the spring of 1973.

	V (hr^{-1}) × 10^2								
	NO_3^-		NH_4^+		H_4SiO_4		V_{DK}/V_{LT}		
Station	V_{LT}	V_{DK}	V_{LT}	V_{DK}	V_{LT}	V_{DK}	NO_3^-	NH_4	H_4SiO_4
3					1.1	1.0			0.91
9					1.7	0.4			0.24
17					13.2	13.5			1.02
20	3.01	0.13	2.19	0.22	2.7	1.7	0.04	0.10	0.63
21	1.54	0.14	1.19	0.37	1.8	0.9	0.09	0.31	0.50
24	1.86	0.45	1.90	0.38	13.0	13.1	0.24	0.20	1.01
27	3.31	0.04			1.8	0.7	0.01		0.39
30	2.07	0.04			13.0	2.5	0.02		0.19
35					3.7	1.9			0.51
38	1.59	0.07			3.5	0.0	0.04		0.00
39	1.08	0.66					0.66		
40			0.81	0.19				0.23	
43	0.21	0.02			3.4	0.4	0.10		0.12
44	0.06	0.04			0.5	0.5	0.67		1.00
45	0.15	0.02	0.55	0.17	0.9	0.3	0.13	0.31	0.33
46			0.63	0.20	0.3	0.1		0.32	0.33
47			0.63	0.46	1.2	0.7		0.73	0.58
48	0.05	0.01			9.0	8.8	0.20		0.98
49			0.96	0.28	4.9	5.4		0.29	1.10
53	0.79	0.05	1.04	0.27	12.5	11.5	0.06	0.26	0.92
58			1.02	0.35				0.34	
59			2.00	0.99	2.0	0.0		0.50	0.00
65			0.69	0.54	2.0	0.0		0.78	0.00
67			0.60	0.08	8.7	9.1		0.13	1.05
71	0.19	0.01	0.31	0.21	7.9	7.9	0.05	0.68	1.00
73	0.19	0.01	0.31	0.21			0.05	0.68	
78			0.48	0.70	8.9	8.8		1.46	0.99
79	0.19	0.01	0.55	0.55	17.4	17.3	0.05	1.00	0.99
82					10.8	9.6			0.89

The V_{DK}/V_{LT} data are summarized statistically in Table 4. At the 99% confidence level (as determined by *t*-test) the mean ratio of dark to light uptake was significantly lower for nitrate than for either ammonium or silicic acid off Baja California. Although the low number of V_{DK}/V_{LT} determinations for nitrate on JOINT I hinders statistical assessment of the difference between mean ratios of dark to light uptake, the dark uptake rate of nitrate was very low at the three stations sampled. The mean V_{DK}/V_{LT} for nitrate was $<5\%$ of that determined for either ammonium or silicic acid.

Table 3. V_{LT}, V_{DK} and V_{LT}/V_{DK} for nitrate, ammonium and silicic acid in seawater collected from the 50% light penetration depth at 24 stations in the upwelling region off northwest Africa in the spring of 1974.

	V (hr^{-1}) $\times 10^2$								
	NO_3^-		NH_4^+		H_4SiO_4		V_{DK}/V_{LT}		
Station	V_{LT}	V_{DK}	V_{LT}	V_{DK}	V_{LT}	V_{DK}	NO_3^-	NH_4	H_4SiO_4
6					1.0	0.0			0.00
13					0.6	0.6			1.00
31					0.2	0.0			0.00
36					1.4	0.4			0.29
38					3.8	0.7			0.18
44					1.9	0.0			0.00
45					0.4	0.1			0.25
52	2.28	0.05	1.13	0.42	1.6	0.7	0.02	0.37	0.44
62	1.80	0.00			0.6	0.1	0.00		0.17
69					0.7	0.7			1.00
70			1.70	0.20	1.1	0.2		0.12	0.18
78	2.60	0.00	1.70	0.52	2.8	0.9	0.00	0.31	0.32
81			2.30	1.00				0.43	
85					2.8	0.7			0.25
89			2.11	0.10	2.6	0.6		0.05	0.23
96			1.74	0.99				0.57	
97			2.16	1.05				0.49	
98			0.97	0.52				0.54	
99					1.2	0.0			0.00
135					0.7	0.0			0.00
138					0.3	0.1			0.33
153					1.0	0.1			0.10
164					3.9	2.1			0.54
175					0.3	0.2			0.67

The mean V_{DK}/V_{LT} for silicic acid was significantly lower off northwest Africa than off Baja California. Within the Baja California system there were three distinct upwelling events during MESCAL II, separated by two periods of weak or poleward winds during which upwelling ceased and a stratified hydrographic was established (Walsh *et al.*, 1977) and Table 4 indicates that the mean value of V_{DK}/V_{LT} for silicic acid in this region was significantly lower during thermally stratified periods than during upwelling periods. Variability in V_{DK}/V_{LT} for silicic acid off northwest Africa, and for nitrate and ammonium in both systems, was not clearly related in time to variability in any measured biological or hydrographic parameter.

At 21 stations off Baja California and five off northwest Africa the ratio of dark to light uptake in populations collected from the 50% light depth was determined for two or more substrates. Data from these stations are presented as plots of

Table 4. Statistical summary of V_{DK}/V_{LT} data presented in Tables 3 and 4.

Region	Substrate	# of Stations	V_{DK}/V_{LT} Highest	Lowest	Mean	Standard Deviation
Baja California	NO_3^-	15	0.67	0.01	0.157	0.207
	NH_4^+	17	1.46	0.10	0.489	0.359
	H_4SiO_4					
	Overall	25	1.10	0.00	0.627	0.390
	Upwelling	16	1.10	0.19	0.800	0.305
	Stratified	9	1.00	0.00	0.319	0.338
Northwest Africa	NO_3^-	3	0.02	0.00	0.007	0.012
	NH_4^+	8	0.57	0.05	0.360	0.191
	H_4SiO_4	20	1.00	0.00	0.298	0.303

Significant *t*-Tests*

Comparison Tested	*t*	Degrees of Freedom	Confidence Level (%)
Mean V_{DK}/V_{LT} lower for NO_3^- than for NH_4^+ off Baja California	3.151	30	99
Mean V_{DK}/V_{LT} lower for NO_3^- than for H_4SiO_4 off Baja California	3.534	38	99
Mean V_{DK}/V_{LT} for H_4SiO_4 lower off northwest Africa than off Baja California	3.105	43	99
Mean V_{DK}/V_{LT} for H_4SiO_4 off Baja California lower during stratified periods than during upwelling periods	3.648	23	99
Mean V_{DK}/V_{LT} lower for NO_3^- than for NH_4^+ off northwest Africa	3.101	9	95

* All other mean V_{DK}/V_{LT} differences between substrates within each region and between regions for each substrate were tested and found not to be significant at the 95% confidence level.

V_{DK}/V_{LT} for nitrate vs. ammonium in Figure 2a, nitrate vs. silicic acid in Figure 2b and ammonium vs. silicic acid in Figure 2c. Figures 2a and 2b reflect the fact that the capacity for dark uptake of nitrate was low at most stations sampled. Figure 2b also shows that the infrequently observed appreciable dark uptake of nitrate occurred only at stations where V_{DK}/V_{LT} for silicic acid was analytically indistinguishable from 1. Thus in this study the few phytoplankton assemblages that showed any appreciable uptake of nitrate in the dark were also able to take up silicic acid in the dark for at least 6 hr at rates undiminished from those at simulated in situ light intensity. Data points in Figure 2c are widely scattered, indicating that while the ratio of dark to light uptake of both ammonium and silicic acid ranged from 0 to 1, there was no apparent tendency for high V_{DK}/V_{LT} values for the two substrates to be observed at the same station.

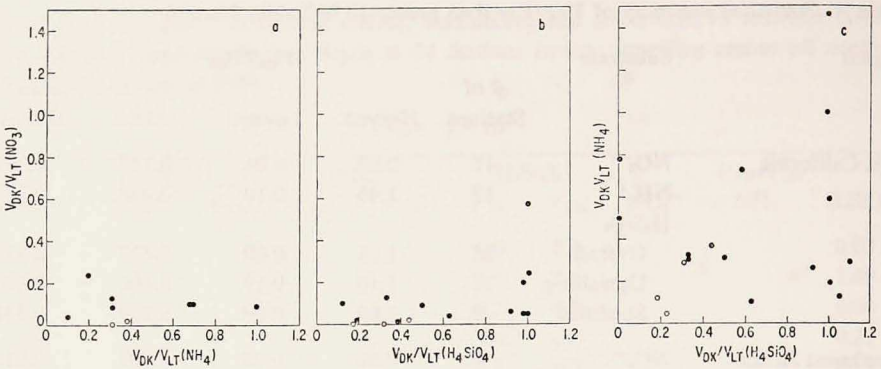

Figure 2. V_{DK}/V_{LT} values for pairs of substrates at the 50% light penetration depth off Baja California (●) and northwest Africa (○). a) nitrate vs. ammonium; b) nitrate vs. silicic acid; c) ammonium vs. silicic acid.

The responses of ammonium and silicic acid uptake to several light intensities in deep and shallow phytoplankton populations at a well-mixed and vertically stratified station off northwest Africa are shown in detail in Figure 3. At the vertically stratified station 62 the responses of ammonium (Figure 3a) and silicic acid (3b) uptake to light intensity were similar: uptake of both substrates was appreciably diminished by darkness in samples from both depths, and the maximum uptake rate was lower for both substrates in the population collected from the greater depth. At the vertically well-mixed station 69, however, ammonium and silicic acid uptake showed a striking difference in their responses to light intensity. The V vs. I curves for ammonium in the deep and shallow populations are virtually identical to one another (3c). Thus, in terms of ammonium assimilation and its response to light, phytoplankton collected from 2m and 55m behaved as replicate samples from a single, homogeneous population. This was not the case for silicic acid (3d): while the population from 55m showed a V vs. I curve similar to that exhibited by both populations at the stratified station, silicic acid uptake by the near-surface population was not detectably diminished at low light intensities or in the dark. As one would expect at a vertically well-mixed station, the populations collected from 2m and 55m at station 69 were indistinguishable from one another with regard to species composition (D. Blasco, personal communication). Thus, populations residing at the two depths appeared identical both taxonomically and in their V vs. I response for ammonium, but an effect of light on silicic acid uptake could be observed only in cells collected from the dysphotic zone.

The kinetic parameters $V_{\max}$ and K_I for nitrate uptake, calculated by fitting equation (1) to the results of nitrate uptake rate versus light intensity experiments listed in Table 1, are presented in Table 5. Equation (1) is applicable only when $V \cong 0$ in the dark, and significant positive values of V_{DK} were frequently observed for

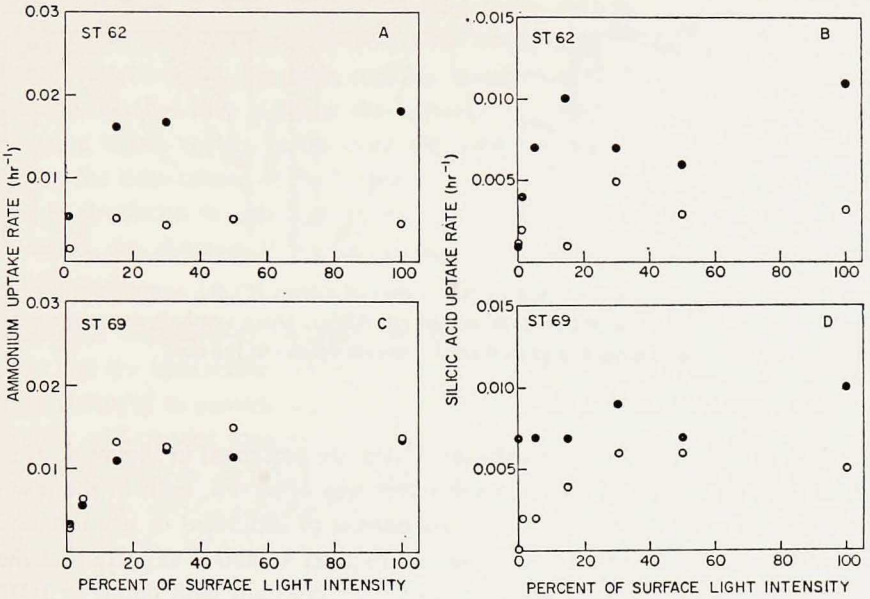

Figure 3. The specific uptake rate of ammonium and silicic acid by phytoplankton collected from the 50% (●) and 0.01% (○) light penetration depths at a vertically stratified station (62) and a vertically well-mixed station (69) off northwest Africa. a) ammonium at station 62; b) silicic acid at station 62; c) ammonium at station 69; d) silicic acid at station 69.

ammonium and silicic acid uptake, so equation (1) was not fitted to ammonium or silicic acid data. Figure 3 shows representative V vs. I data for these two substrates. When an effect of darkness on ammonium or silicic acid uptake rates was observed, it became apparent at light intensities not dramatically different from the K_I values observed for nitrate uptake (i.e. ca. 5-15% of the surface light intensity).

Vertical profiles of nutrient uptake rates at simulated in situ light intensities and

Table 5. V_{max} and K_I values for nitrate uptake from experiments at discrete depths on MESCAL II and JOINT I.

Cruise	Station	Depth (m)	V_{max} (hr^{-1})	K_I (% of Surface Intensity)
MESCAL II	9	2.5	0.020	23.7
	9	5.0	0.019	9.8
	9	9.0	0.010	7.4
	9	18.0	0.020	32.4
	35	3.0	0.031	3.3
	82	16.0	0.011	20.0
JOINT I	85	2.0	0.037	5.5
	85	33.0	0.026	6.2

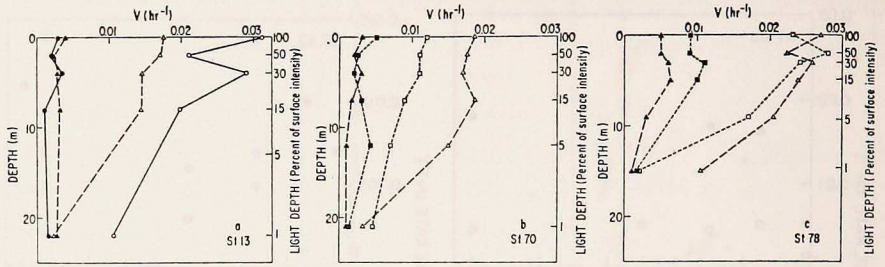

Figure 4. Vertical profiles of the specific uptake rates of nitrate (○,●), ammonium (△, ▲) and silicic acid (□, ■) at three stations off northwest Africa. Open symbols represent uptake at simulated in situ light intensity, and darkened symbols uptake in the dark.

in the dark at three stations off northwest Africa are presented in Figure 4. A strong effect of light on uptake of all three substrates was observed, both in the low rates of dark uptake at all depths and in the diminution of simulated in situ uptake rates between the surface and the 1% light depth. Figures 4a and b indicate that the potential for nutrient uptake in the dark was nearly constant with depth at JOINT I stations 13 and 70, while at station 78 (Figure 4c) dark uptake potential for silicic acid and ammonium decreased markedly from the surface to the 1% light depth. This feature may be related to the fact that the water column was much more stable vertically at station 78 than at stations 13 or 70 where almost neutrally buoyant conditions prevailed (Friebertshauser *et al.*, 1975).

4. Discussion

Interpretation of V_{DK}/V_{LT} values obtained in 6 hr incubations. The ^{15}N and ^{30}Si tracer experiments reported here measured the total amount of substrate taken up during 6 hr incubations, and planktonic algae have been shown to respond physiologically to changes in light intensity on time scales considerably shorter than this (e.g. Eppley and Coatsworth, 1968; Sournia, 1974; Beardall and Morris, 1976). Thus an observed ratio of dark to light uptake can be interpreted as having been constant throughout the incubation only when it approaches either zero or one: when $V_{DK}/V_{LT} \cong 0$, it shows that the dark uptake rate was low throughout the incubation, and when $V_{DK}/V_{LT} \cong 1$, that uptake in the dark was virtually undiminished from that in the light at all times. When V_{DK}/V_{LT} has an intermediate value it reveals little about the instantaneous ratio of dark to light uptake at any given time during the 6 hr incubation, but indicates the relative integrated potential for uptake in the dark over the whole 6 hr interval. Culture experiments with finer time resolution have tended to show that uptake of nitrate and ammonium (Eppley and Coatsworth, 1968; Eppley and Rogers, 1970) and of silicic acid (Nelson *et al.*, 1976; Nelson and Guillard, unpublished) proceed in the dark at undiminished rates

initially, then slow or cease entirely on time scales ranging from minutes to hours. It is likely that transitions of this kind were taking place during our incubations in darkened vessels. Thus, the most realistic interpretation of our observed V_{DK}/V_{LT} values may be that they indicate the approximate fraction of the 6 hr incubation time during which uptake in the dark continued at reasonably undiminished rates. Whatever the time-course of dark uptake, a 6 hr V_{DK}/V_{LT} indicates the fraction of uptake at simulated in situ light intensity that the cells would have been able to carry out in the absence of photosynthesis during the first 6 hr after the samples were collected.

Physiological implications. Nitrate uptake was almost always strongly light dependent and the hyperbolic model of MacIsaac and Dugdale (1972) (equation (1)), appears generally to provide a good fit to nitrate V vs. I data. However, ammonium and silicic acid uptake data are fitted very poorly by the simple hyperbolic model. In the phytoplankton populations examined in these experiments both silicic acid and ammonium uptake exhibited 6 hr responses to light intensity that ranged from the hyperbolic relationship stated by equation (1) to complete light independence (See Table 4). We do not propose any new equation to fit V vs. I data for ammonium or silicic acid. The variability observed in V_{DK}/V_{LT} for these two substrates suggests that the degree to which their uptake rates are affected by the instantaneous ambient light intensity reflects transient, and perhaps rapidly changing, properties of a population. The physiological question raised by phenomena observed in this field study concerns the combination of metabolic capabilities of the cells and hydrographic and optical properties of the near-surface ocean that cause these transitions to take place. Given that the phytoplankton collected at one location and time can assimilate substantial amounts of silicic acid and/or ammonium in the dark, that at another place and time this potential is absent, and that the light responses of silicic acid and ammonium uptake appear to be independent of one another, what processes cause these very large differences to be observed? An adequate physiological explanation of these observed phenomena is not at hand, but some preliminary considerations are discussed below.

Ammonium and nitrate. Uptake of ammonium and nitrate in the dark has been observed previously in laboratory studies (Eppley and Coatsworth, 1968; Eppley and Rogers, 1970; Bhovichitra and Swift, 1977), and in the ocean (Dugdale and Goering, 1967). In the laboratory studies V_{DK}/V_{LT} ranged from 0.37 to 1.05 for ammonium (Eppley and Rogers, 1970) and 0.35 to 0.86 for nitrate (Eppley and Coatsworth, 1968). The field experiments of Dugdale and Goering (1967) yield V_{DK}/V_{LT} values for ammonium and nitrate of 0.25 and 0.10, respectively, in temperate waters and 0.61 and 0.31, respectively, in tropical waters. Thus the capacity for dark uptake of nitrate reported here (Table 4) is similar to that observed previously in temperate phytoplankton, but considerably less than that in tropical phyto-

plankton or in laboratory studies. V_{DK}/V_{LT} values reported here for ammonium vary greatly, but cover the same general range observed in previous studies.

Nitrate uptake by *Skeletonema costatum* has been shown to be an energy-requiring, active transport process during which ATP is consumed (Falkowski, 1975), with cyclic photophosphorylation (Photosystem I), a reaction that proceeds only in the light, the apparent primary ATP source (Falkowski and Stone, 1975). Our field data, showing dark uptake of nitrate to be extremely rare in the natural phytoplankton assemblages we examined, are consistent with the above findings for *S. costatum,* and suggest that an energetic pathway by which nitrate uptake is driven by ATP derived from Photosystem I may be common to many planktonic algae.

Unlike nitrate, ammonium was frequently taken up at high rates in the dark by the natural phytoplankton assemblages we examined. The energetics of ammonium uptake have not been described in detail for planktonic algae, but very large excesses of intracellular over extracellular ammonium concentrations are apparently maintained (e.g. Conover, 1975). Therefore, regardless of the mechanism involved, energy must be expended by the cell to move ammonium nitrogen inward against this strong concentration gradient. In the culture studies mentioned above (Eppley and Coatsworth, 1968; Eppley and Rogers, 1970) the uptake rates of both nitrate and ammonium were initially the same in the dark as in the light, but after 10-20 min the dark uptake rate of nitrate exhibited a substantial decrease. Thus, the light-produced ATP may have become depleted within several minutes in the dark with subsequent uptake of ammonium maintained via either oxidative phosphorylation or substrate-level phosphorylation. The wide variability in V_{DK}/V_{LT} values for ammonium indicates clearly that ammonium uptake is driven by intracellular energetic mechanisms that differ from those supporting nitrate uptake, with no direct dependence on Photosystem I apparent. A more sophisticated physiological interpretation of V_{DK}/V_{LT} data for ammonium in natural phytoplankton should become available as the energetics of ammonium uptake in several planktonic algae are examined in greater detail.

Silicic acid. The potential for dark uptake of silicic acid observed in these experiments on natural phytoplankton populations varied between the very high dark uptake capacity reported for unialgal cultures of *Thalassiosira pseudonana* grown at photosynthetically saturating light intensity (Nelson *et al.*, 1976) and the near lack of such capacity in *Skeletonema costatum* when sub-optimal light conditions were allowed to persist for several days (Davis, 1973). Thus if the ability to take up silicic acid in the dark develops and disappears mainly in response to the production and depletion of stored intracellular energy reserves (Nelson *et al.*, 1976), then the natural phytoplankton populations off Baja California and northwest Africa may generally have been in energetic states intermediate between those of the *T. pseudonana* and *S. costatum* monocultures in the two laboratory experiments. Also silicic

acid uptake by diatoms, unlike other algal nutrient assimilation processes, is confined to a specific period within the cell division cycle, following cytokinesis and preceding the separation of the two daughter cells (Lewin *et al.*, 1966; Eppley *et al.*, 1967). This discontinuous demand for silicon results in tight temporal coupling between silicic acid uptake and cell division (Chisholm *et al.*, 1978), and implies that phytoplankton samples that exhibited high V_{DK}/V_{LT} values for silicic acid in this study contained diatoms that were capable of maintaining nearly undiminished cell-division rates through at least 6 hr of darkness. Using similar reasoning, Nelson and Goering (1978) suggested that actively dividing diatoms probably extended to at least twice the depth of 1% surface light penetration in the Baja California and northwest Africa upwelling regions during MESCAL II and JOINT I.

The observed systematic variability in mean V_{DK}/V_{LT} values for silicic acid (Table 4b) may well reflect differences in the species composition as well as the energetic state of the phytoplankton. Taxonomic and physiological causes of observed effects usually cannot be separated from one another on the basis of field data alone, but the V vs. I responses shown in Figure 3d appear to demonstrate the energetic effect in the absence of species differences. At JOINT I station 69, in a vertically homogeneous water column, phytoplankton collected from 55 m (0.01% surface light) had a V vs. I response for ammonium (Table 3c) and a species composition indistinguishable from those of phytoplankton collected from 2 m (50% light). The only observable difference between the 2 m and 55 m samples was that the population collected from 2 m showed a substantial capacity for dark uptake of silicic acid that was absent in the 55 m population. Thus Figures 3c and 3d combine to indicate both that cells residing at the two depths were in different physiological states resulting from their vertical locations and recent light-exposure histories, and that this difference affected uptake of silicic acid, but not ammonium. If the inability of cells residing at the 0.01% light penetration depth to take up silicic acid in the dark can be interpreted as resulting from depletion of stored energetic reserves between the time of last exposure to near-surface light intensities and the time of collection at 55 m, then this depletion can occur on time scales that are short relative to the rate of vertical mixing, even under the conditions of upwelling and vigorous wind mixing prevalent off northwest Africa during JOINT I.

Ecological implications. Regardless of the physiological mechanisms involved, natural phytoplankton assemblages in the Baja California and northwest Africa upwelling systems were frequently incapable of sustaining ammonium and silicic acid uptake, and always incapable of sustaining nitrate uptake, in the dark for 6 hr at the rate at which they could carry out these processes at saturating light intensity. This result has clear consequences for nutrient uptake in the vigorously wind-mixed, turbid water columns that characterize coastal upwelling regions. Nutrient kinetic studies performed on Baja California and northwest Africa phytoplankton during

MESCAL II and JOINT I indicate that nutrient uptake rates were very rarely limited by substrate availability (Whitledge and Conway, 1977; Nelson and Goering, 1978; Conway and Harmon, unpublished), but the present study shows frequent strong inhibitory effects of darkness on nutrient uptake rates. When these effects are present, they become detectable at ca. 10-15% of the surface light intensity and are quite pronounced at 1% of surface light. Because the wind-mixed surface layer in coastal upwelling regions often extends well beyond the 1% light penetration depth, surface phytoplankton assemblages in these systems are not able to stay within the euphotic zone at all times as they can in most thermally stratified regions of the ocean. The decreased nutrient uptake rates imposed on the phytoplankton by darkened bottles in this study would thus be imposed by the combination of vertical mixing and turbidity over much of the water column below the 10% light penetration depth (ca. 10 m in these studies). It is therefore apparent that the light regime, including both the immediate light intensity and the recent light-exposure history of the phytoplankton, may play a greater role than the nutrient concentration regime in controlling the biological availability of nutrients in coastal upwelling systems, and that this control is characteristically different for each of three major nutrients.

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