

Factors Controlling Phytoplankton Production in Lake Vanda (77°S)

WARWICK F. VINCENT AND CONNIE L. VINCENT

Freshwater Section, Ecology Division, DSIR, Box 415, Taupo, New Zealand

VINCENT, W. F., AND C. L. VINCENT. 1982. Factors controlling phytoplankton production in Lake Vanda (77°S). *Can. J. Fish. Aquat. Sci.* 39: 1602–1609.

At least three floristically distinct communities of algae were distributed down the permanently ice-capped water column of Lake Vanda. Phytoplankton at each depth were highly specialized towards specific conditions of light and temperature. Maximum photosynthesis and algal biomass was at the bottom of the euphotic zone (55–57.5 m) immediately above a region of nutrient-rich anoxic water. This *Phormidium*-dominated community was adapted towards warm temperatures (18–20°C) but a dim light regime. Dissolved inorganic N to P ratios in this region were extreme (>5000:1) and the plankton demonstrated strong cellular P deficiency. A much smaller photosynthetic maximum was recorded in the middle of a large thermohaline convection cell at 25–30 m where P deficiency was less severe, but detectable. A microflagellate community immediately under the ice demonstrated the least response to phosphorus enrichment, but photosynthetic characteristics appeared to be more attuned to the low irradiances which prevail early in the growing season rather than to the relatively bright light regime during midsummer sampling. Algal biomass levels at most depths declined over 4 wk of sampling, further indicating that population maxima are timed early in the season. The low input of phosphorus relative to nitrogen exerts an overall control on phytoplankton biomass in Lake Vanda, but low production rates per unit biomass characterize the shade-adapted populations at all depths.

Key words: phytoplankton, photosynthesis, algal biomass, N to P ratios, ice cap

VINCENT, W. F., AND C. L. VINCENT. 1982. Factors controlling phytoplankton production in Lake Vanda (77°S). *Can. J. Fish. Aquat. Sci.* 39: 1602–1609.

Au moins trois communautés algales, de composition distincte, sont réparties dans la colonne d'eau recouverte de glace en permanence du lac Vanda. Le phytoplancton à chaque profondeur est très spécialisé par rapport à des conditions spécifiques de lumière et de température. La photosynthèse et la biomasse algale sont à leur maximum au fond de la zone euphotique (55–57,5 m), immédiatement au-dessus d'une région d'eau anoxique riche en nutriments. Cette communauté dominée par *Phormidium* est adaptée à des températures élevées (18–20°C) mais à une faible intensité lumineuse. Dans cette région, les rapports N:P inorganiques dissous sont extrêmes (>5 000:1), et le plancton accuse une importante déficience de P cellulaire. Un maximum photosynthétique beaucoup moindre a été enregistré au milieu d'une grande cellule de convection dans la thermocline à 25–30 m où la déficience en P, bien que détectable, est moins sérieuse. Une communauté de microflagellés juste au-dessous de la glace a la plus faible réaction à un enrichissement en phosphore, mais les caractéristiques photosynthétiques semblent plus sensibles aux faibles irradiances du début de la saison de croissance plutôt qu'à l'intensité lumineuse relativement élevée de la mi-été. Les niveaux de biomasse algale à la plupart des profondeurs ont baissé pendant les 4 sem de l'échantillonnage, autre signe que les maxima de population se produisent tôt dans la saison. Les faibles apports de phosphore par rapport à l'azote règlent l'ensemble de la biomasse phytoplanctonique dans le lac Vanda, mais de faibles taux de production par unité de biomasse caractérisent les populations adaptées à l'obscurité à toutes les profondeurs.

Received January 20, 1982
Accepted July 26, 1982

Reçu le 20 janvier 1982
Accepté le 26 juillet 1982

ALMOST 20 years ago Lake Vanda in the Antarctic Dry Valley region was identified as one of the world's clearest and most oligotrophic waters (Goldman et al. 1967). Since that time this permanently ice-covered lake has been the focus of con-

siderable geochemical and geophysical debate (e.g. Hoare 1968; Bydder and Holdsworth 1977; Yoshida et al. 1975) but its biology has remained relatively unexplored. The early investigators on Lake Vanda reported a simple phytoplankton community of low standing crop and productivity, perhaps ultimately limited by temperature and the availability of nitro-

gen; addition of nitrate stimulated photosynthetic CO₂ fixation by both littoral and pelagic samples, and maximum photosynthesis was recorded in the warm, solar-heated, bottom waters of the lake (Goldman et al. 1967).

Subsequent studies on algae in culture and on other meromictic lakes of the Dry Valleys suggest that the controlling effects of temperature and nitrogen require further evaluation. For many species of phytoplankton the ¹⁴C-photosynthesis bioassay appears to be an unreliable and sometimes misleading guide to N or P limitation (Healey 1979). Comparisons between several lakes of South Victoria Land indicate that the low light regime beneath their permanent ice caps may exert a far stronger controlling influence on production per unit biomass than the direct effects of low temperature (Vincent 1981b). The current study was therefore designed to reassess the relative importance of light and temperature, and nitrogen and phosphorus supply for phytoplankton production down the stratified water column of Lake Vanda. We present the first chlorophyll *a* data for Vanda and detail the distribution of algal species with respect to depth over the field season. We then examine the physiological response of phytoplankton from discrete strata to a range of physical and chemical conditions.

Study Site

Lake Vanda (77°35'S, 161°40'E) lies 47 km from the coast, in the Wright Valley, South Victoria Land, at an altitude of 143 m. The lake is 8.5 km long, 2.4 km wide, with a maximum depth relative to the upper ice surface of 68 m. The unusual temperature and salinity characteristics of Lake Vanda were first reported by Armitage and House (1962) and have been the subject of detailed surveys subsequently. Temperatures rise with increasing depth to a maximum of 23.5°C at the bottom of the lake where the conductivity is three times that of seawater. The lake contains several isothermal isohaline layers that are isolated from each other and from the ice surface and lake floor by layers of density-stratified water. Each homogeneous layer is 3 m or less in thickness, with the exception of the thickest band which extends between 17 and 37 m in depth. Within each of these bands strong thermal convection currents maintain homogeneous temperatures and salinities (Hoare 1966, 1968; Ragotzkie and Likens 1964).

Lake Vanda is fed by the Onyx River which carries mid-summer meltwater 40 km inland from coastal piedmont glaciers. The river flows continuously for 1–2 mo each year with a discharge typically around 1 m³·s⁻¹, but with peaks up to 9 m³·s⁻¹ (Chinn 1980).

Methods

Sampling, measurements, and incubations were performed through 10-cm-diameter holes bored through the permanent ice cap. Samples were removed with a 1-L discrete-depth water sampler. Photosynthetically available radiation (PAR) was measured with a Lambda submersible quantum probe fitted with various color filters (blue: Hoya 80B; green: Hoya BX1; red: Vivitar 25A).

TABLE 1. Light extinction properties of Lake Vanda, December 17, 1980. The ice was 330 cm thick at the sampling site. Extinction coefficients for the water are for the region from the lower ice surface to 45 m.

Waveband	Extinction coefficient (m ⁻¹)		% surface irradiance	
	Ice	Water	3.25 m	57.5 m
White	0.59	0.05	14.7	0.7
Red	0.95	0.46	4.5	<0.01
Green	0.50	0.06	19.7	0.6
Blue	0.42	0.04	25.6	1.8

Samples for chlorophyll analysis were filtered through glass fiber filters (grade GF/C) which were stored frozen until extraction by boiling methanol. The extracts were cleared by centrifugation and measured by fluorometry (Holm-Hansen and Riemann 1978). Estimates of chlorophyll *a* were not corrected for degradation products (Talling and Driver 1963).

In vivo fluorescence of chlorophyll *a* was measured with a Turner III fluorometer, with (*F_b*) and without (*F_a*) DCMU as described by Vincent (1980). Cellular fluorescence capacity (CFC) values were calculated (1 - *F_a*/*F_b*) as an index of photochemical capacity per unit chlorophyll (Vincent 1980).

Phytoplankton samples were preserved immediately after collection with Lugol's iodine or 2% (final concentration) glutaraldehyde. The cells were later sedimented and counted by inverted microscopy (Utermöhl 1958).

Photosynthetic rates were measured by in situ incubations in duplicate 60-mL light and dark bottles with [¹⁴C]HCO₃ [35 μCi (1 Ci = 37 GBq) per bottle]. At the end of each 24-h incubation the labeled plankton were filtered onto 0.22-μm Millipore filters. These were acid-fumed for 24 h to remove ¹⁴C-carbonates, air-dried, and counted by liquid scintillation spectrometry. Samples for dissolved inorganic carbon analysis were injected into sealed 30-mL Hypovials and immediately preserved with glutaraldehyde (2% v/v final concentration). The carbon levels were later measured by infrared CO₂ analysis.

Samples for nutrient analysis were filtered through acid-washed glass fiber filters (GF/C) immediately after collection and were stored frozen. All analyses were on a Technicon AutoAnalyzer II as described by Vincent et al. (1981). Total dissolved nitrogen and phosphorus concentrations were measured after ultraviolet light conversion to nitrate and phosphate. Particulate nitrogen and phosphorus were filtered onto acid-washed GF/C filters and stored frozen. This material was subsequently Kjeldahl-digested and then analyzed for phosphate and ammonium.

Three assays for nutrient deficiency were applied to the Lake Vanda plankton. Nitrogen deficiency was tested by the ammonium enhancement assay of Yentsch et al. (1977). When algal cells deficient in nitrogen are enriched with ammonia, they rapidly accelerate their rate of dark CO₂ fixation. Lake Vanda samples were therefore incubated at the depth of collection in dark bottles for 5 h with and without NH₄-N (50 mg·m⁻³ final concentration). Dark carbon uptake was measured with [¹⁴C]HCO₃ as above. As a further guide to both nitrogen and phosphorus demand, lake water samples were incubated for 6 h in situ with an enrichment of nitrogen

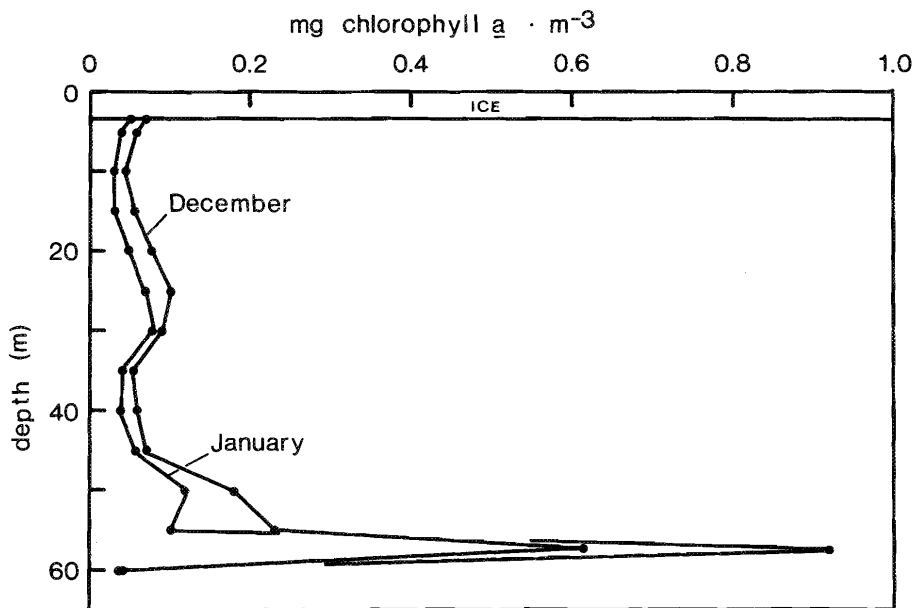


FIG. 1. Distribution of chlorophyll *a* with depth December 13, 1980 and January 11, 1981.

TABLE 2. Photosynthesis in Lake Vanda, December 21–22, 1980. Irradiance values were calculated as the average intensity ($\mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) over the 24-h in situ incubation.

Depth (m)	Photosynthesis ^a	Assimilation number ^b	Photosynthetic efficiency ^c
3.25	130	108	2.6
5	82	83	2.1
15	160	215	6.0
25	223	131	8.0
30	189	104	8.9
40	182	161	17.1
50	463	188	18.2
55	271	90	10.7
57.5	1664	138	27.2
60	Nil		

^aMicrograms C fixed $\cdot \text{m}^{-3} \cdot \text{d}^{-1}$.

^bMicrograms C fixed $\cdot \text{mg}^{-1} \text{chl}a \cdot \text{h}^{-1}$.

^cMicrograms C fixed $\cdot \text{mg}^{-1} \text{chl}a \cdot \text{unit irradiance}^{-1} \cdot \text{h}^{-1}$.

(50 mg $\text{NH}_4\text{-N} \cdot \text{m}^{-3}$) and phosphorus (5 mg $\text{PO}_4\text{-P} \cdot \text{m}^{-3}$). Seston N to P ratios were compared before and after the enrichment (Vincent 1981a). Finally, samples were incubated in situ for 4–6 d in 60-mL light bottles with N, P, N plus P, or no enrichment (levels as above). Photochemical capacity was measured by the CFC index before and after the incubation.

Results

Extinction coefficients for total PAR and blue and green wavebands in the surface waters of the lake approximated the low values obtained by Goldman et al. (1967) almost 20 yr previously (Table 1). The most penetrating waveband measured was blue light; red light was strongly absorbed by the

ice and rapidly extinguished with depth.

Chlorophyll levels (Fig. 1) were very low throughout the water column but rose to a sharp maximum at 57.5 m, just above the anoxic zone (transition from oxic to anoxic water was at 59–60 m). Two less-pronounced maxima were recorded higher in the water column — one immediately beneath the ice, and another between 15 and 35 m, in the center of the large thermohaline convection cell. Between December 13 and January 11, there was a decline in chlorophyll levels at all depths, except at 57.5 m where higher values were recorded in January. In view of the steep chlorophyll gradient at the bottom of the oxygenated water column, this increase may reflect sampling error rather than a real increment in biomass between the two dates. A difference in sampling depth of only a few centimetres could have resulted in a large difference in chlorophyll *a* levels, even on the same day.

In situ photosynthetic rates (Table 2) closely followed the distribution of chlorophyll, with a sharply defined maximum at 57.5 m. Lesser peaks occurred immediately under the ice and at 25–30 m. Assimilation numbers (photosynthesis per unit chlorophyll) demonstrated no marked variation, but light-capturing ability per unit chlorophyll (photosynthetic efficiency) increased with increasing depth to a maximum value just above the oxycline.

Further samples were incubated for 24 h with $[^{14}\text{C}]\text{HCO}_3$ on December 27–28, at 55, 57.5, 60, 62.5, 65, and 67.5 m, with and without DCMU, to test for bacterial photosynthesis. No significant differences between light and dark bottle incubations were recorded in anoxic water below 60 m. Photosynthesis at 55 and 57.5 m was completely eliminated by the DCMU treatment.

Plankton samples from three strata were each incubated with $[^{14}\text{C}]\text{HCO}_3$ at six depths in the lake to determine their relative photosynthetic response to light and temperature. Each assemblage demonstrated maximum rates of photo-

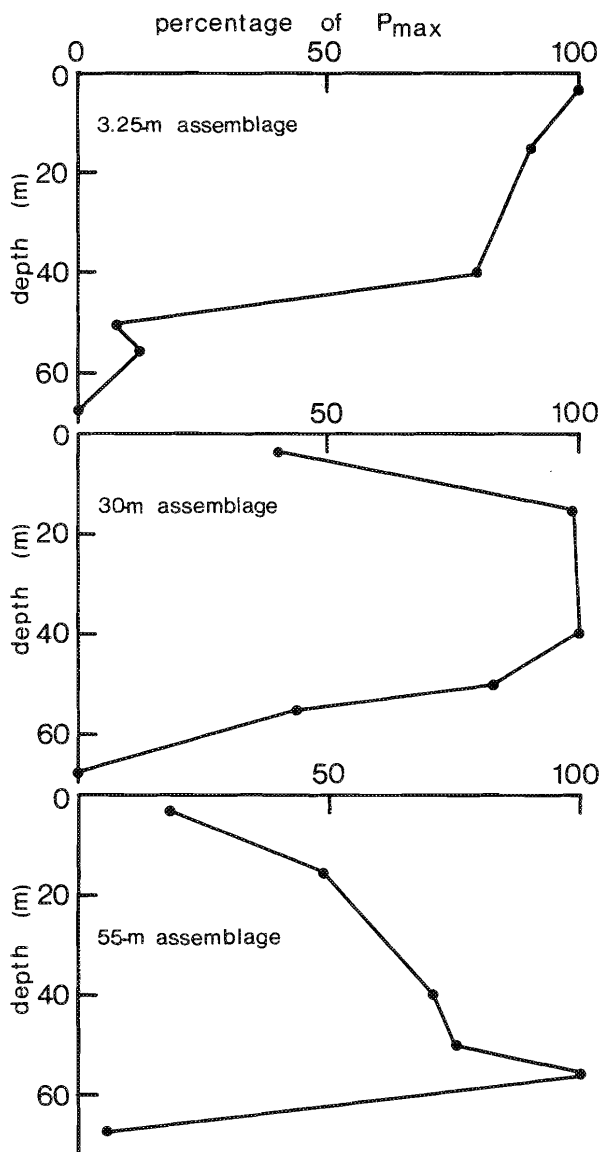


FIG. 2. Effect of displacement on algal photosynthesis December 23–24, 1980. Duplicate light and dark bottles were incubated 24 h at each depth. Rates are expressed as a percentage of the maximum recorded for each assemblage.

synthesis at or close to its depth of collection (Fig. 2) indicating a high degree of specialization towards specific physical conditions. The magnitude and type (positive or negative) of response to displacement were different for each assemblage. Two sets of displacement depths were particularly informative. Between 15 and 40 m (either side of the large convection cell), the temperature variation was almost negligible (6.5 vs. 7.5°C) but light availability changed 3.5-fold, from 8.1 to 2.3% of surface PAR. The 3.25-m assemblage responded to this light decrease by only an 11% drop in photosynthesis. By contrast, the 55-m community was strongly inhibited by the higher light level. The 30-m assemblage

TABLE 3. Cell volumes of phytoplankton dominants in three depth regions of Lake Vanda (— = not detectable).

	Depth (m)	Cell volume ($10^6 \mu\text{m}^3 \cdot \text{L}^{-1}$)	
		Dec. 16	Jan. 11
<i>Ochromonas miniscula</i>	3.25	41.5	33.8
	30	14.5	8.7
	55	—	—
<i>Polytomella</i> sp.	3.25	19.6	0.9
	30	—	—
	55	—	—
<i>Chlorella</i> sp.	3.25	2.5	2.0
	30	3.4	1.5
	55	—	—
<i>Chlamydomonas globosa</i>	3.25	—	—
	30	3.0	1.4
	55	1.9	—
<i>Phormidium fragile</i>	3.25	—	—
	30	76.6	65.1
	55	13.4	13.0
<i>P. antarcticum</i>	3.25	—	—
	30	71.2	38.8
	55	98.5	4.2
<i>P. frigidum</i>	3.25	—	—
	30	—	—
	55	17.6	15.2
<i>Synechocystis</i> (?)	3.25	—	—
	30	—	—
	55	2.9	5.3

TABLE 4. Nitrate–nitrogen and soluble reactive phosphorus (SRP) levels in the Onyx River, December 31, 1980. Each value is the mean for duplicate samples (\pm range) collected 5 min apart.

Site	Distance upstream from Lake Vanda, km	$\text{NO}_3\text{-N}$ ($\text{mg} \cdot \text{m}^{-3}$)	SRP ($\text{mg} \cdot \text{m}^{-3}$)
1	6	51.5 ± 2.0	3.2 ± 1.1
2	4	35.8 ± 0.9	1.7 ± 0.1
3	2	28.6 ± 0.6	0.6 ± 0.1

demonstrated no difference in response to incubation at the two depths suggesting a wide adjustment to this range of intensities. A second useful comparison was between the incubations at 50 and 55 m. Over this 5-m-depth interval, light availability changed very little (1.2–0.9% of surface PAR) but temperatures increased by 6°C (12.5–18.5°C). Photosynthesis by the 55-m sample dropped by 25% when displaced from its depth of collection to 50 m. A reverse response was demonstrated by the 30-m assemblage for which photosynthetic rates were 89% higher at 50 m relative to 55 m. Photosynthesis by the 3.25-m community was very low (<15% of optimum) at both 50 and 55 m, and there was no significant difference between the two incubations.

Phytoplankton samples from strata containing the three assemblages tested by displacement were examined by Utermöhl microscopy. The three communities differed markedly in species composition (Table 3). Microflagellates were conspicuous components of the two upper assemblages, but at the

TABLE 5. Seston and dissolved inorganic N to P ratios (wt/wt), and ammonium enhancement response. *F* values are for the difference between dark CO₂ fixation with and without ammonium additions. Values less than 2.92 are not significant at *P* > 0.1 (df = 2) (— = not tested).

Depth (m)	Seston			Dissolved inorganic N/P ^a	Ammonium enhancement (<i>F</i> values)
	Nitrogen (mg · m ⁻³)	Phosphorus (mg · m ⁻³)	N/P		
3.25	10.2	0.8	12.8	70	0.16
15	3.7	0.2	18.5	39	1.21
25	9.8	0.6	16.3	104	0.87
35	7.0	0.2	35.0	84	—
45	5.7	0.3	19.0	103	0.83
50	7.8	0.4	19.5	4978	—
55	10.5	0.2	52.5	>52 912	<0.01
57.5	17.5	0.4	43.7	5982	—
60	26.2	0.2	131.0	2100	—

^aInorganic N/P = (NO₃-N plus NO₂-N plus NH₄-N)/(soluble reactive P). Complete data set for inorganic nutrients presented in Vincent et al. 1981.

bottom of the euphotic zone blue-green algal populations dominated.

The single inflow to Lake Vanda, the Onyx River, was sampled at its point of entry to the lake within the period of peak flow (late December). The total dissolved nitrogen level was 178 mg · m⁻³ (range for duplicate samples of ±16) and total dissolved phosphorus was 2.9 ± 0.1. This high ratio of N to P load (61.5:1) suggested that phosphorus might be in relatively short supply for phytoplankton growth in the lake. A comparison of nitrate and soluble reactive phosphorus (SRP) levels further up the river demonstrated a similarly high ratio of N to P with some evidence of nutrient stripping by stream biota before discharge to the lake (Table 4). Between sites 1 and 3 there was no change in discharge but the nitrogen and phosphorus fell by 8.8:1, which closely approximates the ratio found in algal tissue.

Dissolved inorganic N to P ratios in the surface waters of Lake Vanda (Table 5) reflected those within the Onyx River. At the bottom of the euphotic zone the ratio increased to extreme values dictated primarily by an accumulation of nitrate produced by nitrifier activity (details in Vincent et al. 1981). Particulate levels of phosphorus were very low throughout the water column. The ratio of nitrogen to phosphorus in the seston similarly increased with increasing depth to very high values at the bottom of the euphotic zone.

No stimulation of dark CO₂ fixation by addition of ammonia was recorded for any depth assayed (Table 5). Seston N to P ratios dropped in all samples incubated with a nitrogen plus phosphorus enrichment, but the decrease was statistically significant for only the 30-m assemblage (Table 6). This response contrasted with a sample tested at the same time from Lake Fryxell, a more productive lake in the adjacent valley. The seston from just under the ice in Fryxell selectively accumulated nitrogen from a N plus P enrichment, and the seston N to P ratio significantly increased.

The photochemical response to nutrient enrichment was measured by CFC assays on further plankton samples from three strata. After 2 d the 55-m samples demonstrated significantly increased CFC values in response to phosphorus enrichment, but in those samples incubated with nitrogen, CFC

was reduced relative to the control (Table 7). There was a significant decrease in the control (no nutrients) over this period indicating an adverse effect of containerization on this bottom euphotic assemblage. At higher depths in the water column there were no significant changes in CFC over the first 2 d and the in situ incubations were therefore extended for 2 more days. By day 4 there was a positive response to phosphorus by the 30-m, but not the 3.25-m assemblages. In both sets of samples enriched with nitrogen, there was a significant decline in CFC. The final CFC controls for both depths did not change over the course of the incubation.

Discussion

Nitrogen has been identified as the primary nutrient limiting algal production in several Antarctic lakes. However, the supporting evidence for these observations has generally been sparse and derived from a restricted array of measurements and methodologies. The photosynthetic CO₂ fixation response to nitrate enrichment reported for Vanda (Goldman et al. 1967) has been recorded in Lake Skallen Oike (69°40'S, 39°24'E) where SRP levels were relatively high (Tominaga 1977). Hand and Burton (1981) reported undetectable levels of dissolved inorganic nitrogen, but abundant phosphorus in Ace Lake in the Vestfold Hills (68°28'S, 78°11'E). From this they concluded that algal production may depend upon the rate of supply of inorganic nitrogen by meltwater to the lake each summer. In Lake Fryxell, in the adjacent valley to Lake Vanda, water samples from immediately under the ice contained low levels of inorganic N, and the plankton responded positively to ammonium enrichments by enhanced dark CO₂ fixation and increased photochemical capacity as measured by CFC (Vincent 1981b). Selective accumulation of nitrogen by the Fryxell plankton from an N plus P enrichment reported in the present study provides supportive evidence for a persistent shortage of nitrogen relative to phosphorus for algal growth in that lake.

We could find no evidence of nitrogen limitation in Lake Vanda. Nitrogen was in abundant supply relative to phosphorus, both within the meltwater inflow and within all strata

TABLE 6. Seston N to P ratios before and after 6 h enrichment with 50 mg $\text{NH}_4\text{-N}\cdot\text{m}^{-3}$ plus 5 mg $\text{PO}_4\text{-P}\cdot\text{m}^{-3}$. Each value is for duplicate samples \pm range. *t* values test the significance of change for each lake water.

	Lake Vanda			Lake Fryxell
	3.25 m	30 m	55 m	4.5 m
Seston N/P (initial)	19.3 \pm 2.2	20.2 \pm 0.2	48.4 \pm 7.7	10.6 \pm 0.2
Seston N/P (final)	17.6 \pm 2.6	17.6 \pm 0.3	23.6 \pm 5.7	15.2 \pm 1.5
<i>t</i> -value	0.5	7.2	2.6	3.5
probability	>0.1	<0.025	>0.1	<0.1

beneath the ice. Dissolved inorganic N to P ratios were well in excess of 15 to 1 at all depths. No ammonium enhancement of dark CO_2 fixation was recorded in any sample tested. Photochemical capacities of the three separate assemblages (3.25, 30, 55 m) were not stimulated by enrichment with ammonium, but in fact for two of the communities tested there was a significant reduction in CFC relative to the control during the plus N incubation.

Several lines of evidence favor phosphorus as the primary nutrient limiting algal growth in Lake Vanda. SRP concentrations were very low in the Onyx River and appeared to be further reduced by biological stripping before discharge to the ultra-oligotrophic surface waters of the lake. At all depths between the lower ice surface and 55-m lake water, SRP values were less than 1 $\text{mg}\cdot\text{m}^{-3}$ (Vincent et al. 1981). Particulate phosphorus levels were similarly low, and the seston N to P ratio at most euphotic depths was in excess of the typical range found in algae growing under nutrient sufficient conditions. This ratio dropped upon N plus P enrichment as phosphorus but not nitrogen was accumulated by the plankton, thereby demonstrating a higher demand for P relative to N. Both the 30- and 55-m samples significantly increased their photochemical capacity during enrichment with P.

Both rapid physiological and longer-term bioassays for nutrient demand and deficiency must be interpreted with caution. The former are highly sensitive to recent light and nutrient history, and physiological transients; the latter are prone to artifacts of containerization (Vincent 1981a). However, the assay responses reported here from a variety of time scales (hours to days) consistently indicate a shortage of phosphorus relative to nitrogen for plankton primary production. This finding is strongly supported by the direct analyses of particulate material and dissolved nutrients.

Historically distinct communities of phytoplankton occupied different depth regions of Lake Vanda where they were highly specialized towards the specific conditions of light and temperature, and probably nutrient supply and salinity, within each layer. Like other lakes of the region (Vincent 1981b), maximum biomass and photosynthesis occurred just above the interface between oxic water and the nutrient-rich anoxic zone. The blue-green algae which dominated this community did not appear to be photosynthetically active in the deeper, anaerobic layers, as they are in some meromictic lakes (e.g. Solar Lake, Cohen et al. 1977). In the region of maximum chlorophyll, SRP levels were higher than in the rest of the

euphotic zone (from 0.6 $\text{mg}\cdot\text{m}^{-3}$ at 56 m to 3.1 $\text{mg}\cdot\text{m}^{-3}$ at 59 m). Temperatures were warm (20°C) by comparison with higher depths and more typical of temperate lakes in summer. However, the stimulatory effects of temperature were probably offset by low light availability (<1% of surface irradiance), and productivity per unit biomass was as low in the deep euphotic zone as it was in the cooler waters immediately beneath the ice.

Deep chlorophyll maxima are a ubiquitous feature of thermally stratified euphotic zones (Richerson et al. 1978) and are often particularly striking in the highly stable waters of meromictic lakes (e.g. Cohen et al. 1977). In the Canadian Experimental Lakes Area (ELA) metalimnetic algal maxima have been attributed to slow rates of loss (respiration, grazing, sedimentation) rather than elevated rates of production (Fee 1976). Like other permanently ice-capped lakes of the Dry Valleys, Lake Vanda contains no crustacean zooplankton (Goldman et al. 1967; W. F. Vincent personal observation) and grazing losses cannot be considered a determinant of algal distribution. The deep production zone of Vanda is uniquely a region of minimal energy input yet highest euphotic temperatures under which respiratory losses may be maximal. Sedimentation may also be more rapid than in the thermohaline convection cells higher in the water column. In marked contrast to ELA maxima, the deep biomass peak in Lake Vanda must be considered a community of elevated gross production rates, favored by the relative abundance of nutrients across the oxycline, with loss rates that are probably higher than in other euphotic strata.

A community of microflagellates and *Phormidium* dominated the middle euphotic zone where the phytoplankton appear to be retained and concentrated in the center (25–30 m) of the large thermohaline convection cell. In this region both chlorophyll *a* and photosynthetic rates were higher than in the overlying water despite lower irradiances. The center of this convective layer may resemble Stommel's (1949) "zone of retention" in Langmuir circulation cells where algal sedimentation is greatly reduced by horizontal and vertical water movements. Phosphorus deficiency in this region was less severe than in the deep euphotic zone, but seston N to P ratios were high and responded to P enrichment.

Immediately beneath the ice, temperatures rose from 0 to 4.5°C within several centimetres deep. This density gradient may aid the microflagellates which dominate the upper euphotic community in maintaining their position. Phosphorus

TABLE 7. Photochemical response to enrichment, as measured by DCMU-induced fluorescence of chlorophyll (CFC index). Each value is the mean for duplicate lake water samples incubated for 2 d (55 m) or 4 d (3.25 and 30 m) at the depth of collection with 50 mg · NH₄-N · m⁻³, 5 mg PO₄-P · m⁻³, or no addition (control). Numbers in parentheses are *F* values for orthogonal comparisons between the control and treatment CFC. *F* values greater than 7.7 are significant at the *P* < 0.05 level (df = 1, 4).

Depth (m)	CFC units			
	Initial	Control	Plus N	Plus P
3.25	0.271 (<0.01)	0.272	0.179 (11.08)	0.262 (<0.01)
30	0.192 (0.04)	0.200	0.077 (18.96)	0.334 (25.30)
55	0.358 (10.62)	0.214	0.163 (1.31)	0.547 (56.95)

availability may be slightly higher in this region as a result of freeze concentration of salts as the ice cap thickens over winter, and the inflow of Onyx River water under the ice during summer. In this region of the water column, seston N to P ratios were lowest and there was no clear evidence of strong cellular P deficiency.

The ice cap covering Lake Vanda is relatively thin and highly transparent compared to other Dry Valley lakes, e.g. in Lake Fryxell 1% of surface irradiance penetrates the ice (Vincent 1981b), cf. 15% in Vanda (Table 1). Light-capturing efficiency was understandably less in Lake Vanda relative to Fryxell; however, the Vanda populations do appear to be more shade-adapted than ambient light levels would suggest. Immediately under the ice the average irradiance over 24 h in early January was 130 μE · m⁻² · h⁻¹. This lies within the range generally considered optimal for algal photosynthesis (e.g. Harris 1978), yet photosynthetic rates per unit chlorophyll in Vanda were still very low at these upper euphotic depths (ca. 0.1 mg C · mg⁻¹ chl *a* · h⁻¹) by comparison with those rates typical of temperate latitudes (1–10 mg C · mg⁻¹ chl *a* · h⁻¹). From 3.25 m to 40 m there was an 84% decrease in light intensity (temperature rose only 3°C), yet displacement of the phytoplankton from the upper to lower depth resulted in only a 20% drop in photosynthetic rates. These observations suggest that the sub-ice community was adapted to lower light levels than those measured during the period of sampling.

Between mid-December and mid-January there was a marked decline in chlorophyll *a* levels and in cell biomass of all but one of the phytoplankton dominants. This is consistent with previous observations on Lake Fryxell (Vincent 1981b): phytoplankton maxima in these lakes are probably timed very early in the season after nutrients have accumulated to a maximum over winter (mineralization by bacteria, diffusion from the anoxic zone, freeze-concentration at the ice-water interface) and when ambient irradiances have just begun to rise above the compensation point for algal photosynthesis. The most successful phytoplankton species in these lakes may therefore be shade-adapted forms capable of efficiently capturing the low irradiances in spring to take up and store a very limited supply of nutrients. The shade characteristics of Vanda sub-ice populations, living under relatively bright light

conditions in midsummer, is supportive evidence of an early season phytoplankton maximum. During the brief 2–3 mo that this portion of Antarctica is accessible to limnologists, the primary production of Dry Valley lakes has passed its peak, and the planktonic algae are in decline. These populations demonstrate a physiology more attuned to irradiance conditions prevailing during early season growth than to the light regime experienced over the period of midsummer sampling. Thus low light appears to have a more controlling effect on productivity per unit biomass than temperature, but in Lake Vanda phosphorus availability exerts an overall control on production by limiting algal biomass.

Phytoplankton concentrations in Lake Vanda are comparable with ultra-oligotrophic waters in the Canadian Arctic. In Char Lake (74°42'N, 94°50'W), chlorophyll *a* values fall within the range 0.1–0.7 mg · m⁻³ (Kalf and Welch 1974); in Lake Vanda upper euphotic concentrations were typically less than 0.1 mg chlorophyll *a* · m⁻³, but rose to 0.7–0.9 mg · m⁻³ in the region of the deep production peak. In both Vanda (this study) and Char Lake (Rigler 1978), phosphorus appears to exert a stronger constraint on algal biomass than nitrogen; however, the controls on production per unit biomass (P/B) appear to differ markedly between the two systems. The cold temperatures of Char Lake depress P/B to a maximum assimilation number of 225 μg C · mg⁻¹ chlorophyll *a* · h⁻¹ (Kalf and Welch 1974). In Lake Vanda, temperatures attain higher values more typical of temperate lakes, yet assimilation numbers are all lower than in this northern counterpart. In Lake Vanda, and probably other ice-capped lakes of Antarctica, rates of community metabolism per unit biomass appear to be limited by low energy input to the euphotic zone, rather than by low temperatures more typical of Arctic waters studied to date.

Acknowledgments

We thank Ms K. Law for technical assistance, Antarctic Division DSIR, and the U.S. Navy for logistic support in the field; Drs T. Torii, S. Nakaya, W. Green, and D. Canfield for useful discussions; Drs E. White, M. Timperley, and G. Coulter for critically reviewing the manuscript; and Ms J. Simmiss for typing each draft. Fieldwork was performed during the 1980–81 New Zealand Antarctic Research Programme.

- ARMITAGE, K. B., AND H. B. HOUSE. 1962. A limnological reconnaissance in the area of McMurdo Sound, Antarctica. *Limnol. Oceanogr.* 7: 36–41.
- BYDDER, E. C., AND R. HOLDSWORTH. 1977. Lake Vanda (Antarctica) revisited. *N.Z. J. Geol. Geophys.* 20: 1027–1032.
- CHINN, T. J. 1980. Hydrological Research Report, Dry Valleys, Antarctica 1974–75. Ministry of Works and Development, Christchurch, N.Z. 54 p.
- COHEN, Y., W. E. KRUMBEIN, AND M. SHILO. 1977. Solar Lake (Sinai) 2. Distribution of photosynthetic microorganisms and primary production. *Limnol. Oceanogr.* 22: 609–620.
- FEE, E. J. 1976. The vertical and seasonal distribution of chlorophyll in lakes of the Experimental Lakes Area, northwestern Ontario: implications for primary production estimates. *Limnol. Oceanogr.* 21: 767–783.
- GOLDMAN, C. R., D. T. MASON, AND J. E. HOBBIE. 1967. Two antarctic desert lakes. *Limnol. Oceanogr.* 12: 295–310.
- HAND, R. M., AND H. R. BURTON. 1981. Microbial ecology of an

- Antarctic saline lake, p. 363–384. *In* W. D. Williams [ed.] Salt lakes. Junk, The Hague.
- HARRIS, G. P. 1978. Photosynthesis, productivity and growth: the physiological ecology of phytoplankton. *Ergeb. Limnol.* 10: 1–171.
- HEALEY, F. P. 1979. Short-term responses of nutrient deficient algae to nutrient addition. *J. Phycol.* 15: 289–299.
- HOARE, R. A. 1966. Problems of heat transfer in Lake Vanda, a density stratified Antarctic Lake. *Nature* 210: 787–789.
1968. Thermohaline convection in Lake Vanda, Antarctica. *J. Geophys. Res.* 73: 607–618.
- HOLM-HANSEN, O., AND B. RIEMAN. 1978. Chlorophyll *a* determination: improvements in methodology. *Oikos* 30: 438–447.
- KALFF, J., AND H. E. WELCH. 1974. Phytoplankton production in Char Lake, a natural polar lake, and in Meretta Lake, a polluted polar lake, Cornwallis Island, Northwest Territories. *J. Fish. Res. Board Can.* 31: 621–636.
- RAGOTZKIE, R. A., AND G. E. LIKENS. 1964. The heat balance of two Antarctic lakes. *Limnol. Oceanogr.* 9: 412–425.
- RICHERSON, P. J., M. M. LOPEZ, AND T. COON. 1978. The deep chlorophyll maximum layer of Lake Tahoe. *Verh. Int. Verein. Theor. Angew. Limnol.* 20: 426–433.
- RIGLER, F. H. 1978. Limnology in the high Arctic: a case study of Char Lake. *Verh. Int. Verein. Theor. Angew. Limnol.* 20: 127–140.
- STOMMEL, H. 1949. Trajectories of small bodies sinking slowly through convection cells. *J. Mar. Res.* 8: 24–29.
- TALLING, J. F., AND D. DRIVER. 1963. Some problems in the estimation of chlorophyll *a* in phytoplankton, p. 142–146. *In* M. S. Doty [ed.] Proceedings of a Conference on Primary Productivity Measurement, Marine and Freshwater. U.S. Atomic Energy Commission, Washington, D.C.
- TOMINAGA, H. 1977. Photosynthetic nature and primary productivity of Antarctic freshwater phytoplankton. *Jpn. J. Limnol.* 38: 122–130.
- UTERMÖHL, H. 1958. Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. *Mitt. Int. Verein. Theor. Angew. Limnol.* 15: 796–804.
- VINCENT, W. F. 1980. Mechanisms of rapid photosynthetic adaptation in natural phytoplankton communities. II. Changes in photochemical capacity as measured by DCMU-induced chlorophyll fluorescence. *J. Phycol.* 16: 568–577.
- 1981a. Rapid physiological assays for nutrient demand by the plankton I. Nitrogen. *J. Plankton Res.* 3: 685–697.
- 1981b. Production strategies in antarctic inland waters: phytoplankton eco-physiology in a permanently ice-covered lake. *Ecology* 62: 1215–1224.
- VINCENT, W. F., M. T. DOWNES, AND C. L. VINCENT. 1981. Nitrous oxide cycling in Lake Vanda, Antarctica. *Nature* 292: 618–620.
- YENTSCH, C. M., C. S. YENTSCH, AND L. R. STRUBE. 1977. Variations in ammonium enhancement, an indication of nitrogen deficiency in New England coastal phytoplankton populations. *J. Mar. Res.* 35: 537–555.
- YOSHIDA, Y., T. TORII, Y. YUSA, S. NAKAYA, AND K. MORIWAKI. 1975. A limnological study of some lakes in the Antarctic, p. 311–320. *In* R. P. Suggate and M. M. Cresswell [ed.] Quaternary studies. Royal Soc. N.Z., Wellington, N.Z.