

Microbial communities in southern Victoria Land streams (Antarctica)

I. Photosynthesis

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Abstract

The glacier-fed ephemeral streams of southern Victoria Land (*ca.* 78° S, 164° E) are colonised by an epilithon dominated by cyanobacterial mats and films. Biomass levels are often high ($> 15 \mu\text{g Chl } a \cdot \text{cm}^{-2}$). The mat structure, pigment and photosynthetic characteristics of these communities have been investigated on site. The mats in high light environments have a layered structure with high levels of light shielding accessory pigments in the upper layers and elevated chlorophyll *a* and phycocyanin concentrations in the lower layers. Photosynthetic rates per unit area ($0.4\text{--}3.5 \mu\text{g C} \cdot \text{cm}^{-2} \cdot \text{hr}^{-1}$) fall within the range reported for temperate communities. *P vs. I* curves were used to separate high, intermediate and low light communities. I_k values for high light communities were at or lower than PAR recorded at midnight in the polar midsummer (*ca.* $100 \mu\text{E m}^{-2} \cdot \text{s}^{-1}$). We did not detect photoinhibitory responses at the midday light intensities. *In situ* continuous nutrient enrichment experiments failed to demonstrate N or P limitation to pigment content or photosynthetic rates. We suggest that the growth of these communities is controlled by factors other than light and nutrients.

Introduction

Rivers and streams are a common feature of the coastal ice-free areas of Victoria Land in Antarctica. These southern polar streams are derived from melting glaciers and typically flow for several weeks during mid-summer (Vincent & Howard-Williams, 1986). Where slopes are not too steep and channel beds are relatively stable, a dense epilithic community can develop. This is dominated by cyanobacteria with associated heterotrophic bacteria, fungi and a few microherbivores. A large proportion ($> 50\%$) of the biomass of the summer epilithic communities remains in a frozen but viable state over the 10 months or so of the year when the streams do not flow and the chan-

nels are dry. This period includes the Antarctic winter when temperatures in this area fall to -55°C .

With the onset of glacier melt, and the presence of flowing water in the stream channels the dry frozen epilithic communities respond to rewetting rapidly (Vincent & Howard-Williams, 1986, 1987) and within 30 minutes H^{14}CO_3 label enters a wide range of photosynthetic end products including low molecular weight compounds, protein and polysaccharides. However, although the cyanobacteria can re-initiate metabolism rapidly on rehydration, full recovery of the populations to streamflow conditions is much slower. A time frame of days to weeks is required.

A previous study (Vincent & Howard-

Williams, 1986) demonstrated rates of gross photosynthesis for the midsummer epilithon of *ca.* $1-2 \mu\text{g C cm}^{-2} \text{hr}^{-1}$ of which a variable but generally high proportion was consumed in respiration. On the basis of colonisation experiments on artificial substrates in several of the streams of different nutrient status we hypothesised that nutrients and light were unlikely to be controlling factors in the productivity of the epilithon although Goldman *et al.* (1972) had suggested that the marked photoinhibition they detected in pond algal mats in the area could repress daily photosynthetic rates.

The aims of this study were to examine in more detail the pigment composition and photosynthetic characteristics of the stream communities and attempt to better quantify the primary control on photosynthesis. To this end we report here on the specific effects of variable light intensity and nutrient regimes on pigment composition and photosynthetic rates.

Study sites

Experiments and field sampling were carried out at three sites in the McMurdo Sound area (78°S , 164°E). These were the Adams and Fryxell streams and the Onyx river. All these typically flow from mid December to late January or early February. Some typical environmental features are listed in Table 1. Flows are highly variable

both diurnally, with the streams often reduced to a trickle between 2400 and 0600 hrs, and over longer time scales when days of warm weather can cause large volumes of water to discharge from the glaciers. Conversely cold weather can stop flow completely. Like discharge, nutrient concentrations are very variable with highest levels occurring at lowest discharge during freeze periods. The Fryxell stream was found to contain among the lowest nutrient concentrations in a wide range of streams we have examined (Howard-Williams *et al.*, 1986b). The algal communities of the streams typically consisted of;

- *Nostoc* dominated mats and films in seepage areas near glacier faces and on moist ground where water flows very slowly.
- Dark 'crusts' of *Gloeocapsa* and *Schizothrix* occur on upper surfaces of rocks and are particularly abundant at or near the water line.
- Mat communities in stream channels dominated by *Phormidium*, *Oscillatoria*, *Lyngbya*, *Microcoleus* and *Schizothrix* (Broady, 1982). These mats are the most common type of epilithic community and occur on and between rocks, across pebble beds and gravels. Typically the mats are brown pink or orange.
- Green or grey green or yellow green filaments and mats of *Prasiola calophylla*, *Tribonema* sp., *Binuclearia tectorum* and *Oscillatoria* spp. occur in crevices between large boulders or beneath

Table 1. Selected environmental features of three south Victoria Land streams (Data from Howard-Williams *et al.*, 1986a, 1986b). ND = not detectable.

	Adams	Fryxell	Onyx	Alph
Length (km)	2.7	2	30	12
Midseason discharge* $\text{m}^3 \text{s}^{-1}$	0.15	0.06	1.1	1.0
Suspended sediments g m^{-3}	8	2	27-131	5
Nutrients midseason				
Upstream				
DRP mg m^{-3}	28	6.5	0.3	12.1
$\text{NH}_4\text{-N}$ mg m^{-3}	35	1.5	2	3.4
$\text{NO}_3\text{-N}$ mg m^{-3}	46	17.6	13	5.1
Downstream				
DRP mg m^{-3}	5.4	0.2	1.9	12.3
$\text{NH}_4\text{-N}$	8.5	ND	8.0	2.8
$\text{NO}_3\text{-N}$	7.5	2.0	4.0	1.3

* Daily maximum

DRP = Dissolved Reactive Phosphorus

boulders in fast flowing water where sediments cannot accumulate.

The biomass dominants were *Nostoc*, *Phormidium*, *Binuclearia* and *Prasiola* and our experiments concentrated upon these communities.

Methods

Environmental measurements

Stream temperatures were measured with a YSI combined O₂-temperature probe and solar radiation as photon flux density in the 400–700 nm waveband with a LiCor Instruments sensor LI 190 and meter LI 185. Stream discharges were obtained from velocity profiles obtained with a Teledyne Gurley pygmy current meter. Water for nutrient analyses was filtered on site through pre-rinsed Whatman GF/C filter papers stored frozen and later analysed by Technicon Auto-Analyser (Howard-Williams *et al.*, 1986b).

Biomass, pigments and tissue analyses

Samples of epilithon were collected by small plastic syringe corers and kept frozen in storage in the dark until return to New Zealand. Dry weight, ash free dry weight and % carbon were analysed as in Vincent & Howard-Williams (1986). Tissue N and P analyses were done by Technicon Auto-Analyser following acid digestions.

Extracts of the core samples for chlorophyll *a* were made with dimethylsulphoxide at room temperature (15–20 °C) for 24 hrs and then assayed by the method of Shoaf & Lium (1976). Pigment scans were run from 350–750 nm on a Cary dual beam recording spectrophotometer blanked against dimethylsulphoxide/acetone mix. Relative carotenoid concentrations were expressed as the ratio of the extinction at 480 nm (Strickland & Parsons, 1968) to that at 663 nm. Phycocyanin extracts were made on an aqueous extract of cell material following maceration in a tissue grinder and then cell rupture with glycerol/distilled water (Wyman & Fay, 1986). Concentrations were determined on an Aminco scanning spectrofluorometer against prepared C-phycocyanin standards.

Carbon dioxide exchange

Cores of the epilithon were placed in 30 ml Universal vials with a covering of 2–3 ml of stream water and sealed with a rubber septum and screw cap. The vials were connected with a Binos portable Infra-Red Gas Analyser (IRGA) set up on site at the stream (Vincent & Howard-Williams, 1986). The IRGA was set up in a differential closed circuit configuration. Field calibration was done with two CO₂/air standards prepared by the laboratory of New Zealand Industrial Gases Ltd.

Field experiments

(a) *Low light intensity and pigment composition.* A 0.25 m² area of 95% shade cloth was placed over intact *Phormidium* mats in the Fryxell stream, and at 0, 2, and 4 days, triplicate core samples were collected from the sunlit and shaded portions of the stream for analysis.

(b) *Photosynthesis vs. Irradiance (P vs. I).* Experiments were conducted on several mat communities. Sample and reference vials of the IRGA set up were placed in a series of shade cloths in stream water (temperatures 5–8 °C). The light series was 100% (full sun), 60%, 36%, 27%, 16%, 10%, 6%, 2%, 1% and 0% (darkness). The IRGA system was flushed out after each shade incubation to ensure an adequate CO₂ supply in high light and to prevent a CO₂ buildup in low light. Ambient photon flux density and temperature were monitored throughout the experiments.

(c) *The effects of nutrient supply.* The experiment was a 9 day incubation of several epilithic communities in flow through enrichment tubes placed in the middle of the bed of Fryxell stream. The design closely followed that of Peterson *et al.* (1983) except that in the shallow Fryxell stream we could place the clear plexiglass tubes on the stream bed (Plate 1). Continuous enrichment with dissolved inorganic N (final concentration 200 mg N m⁻³) or dissolved reactive phosphorus (final concentration 20 mg DRP m⁻³) or both together was maintained with 3 litre reservoirs coated in black, which discharged through a 4 mm tube to a tip of fine calibrated auto-analyser

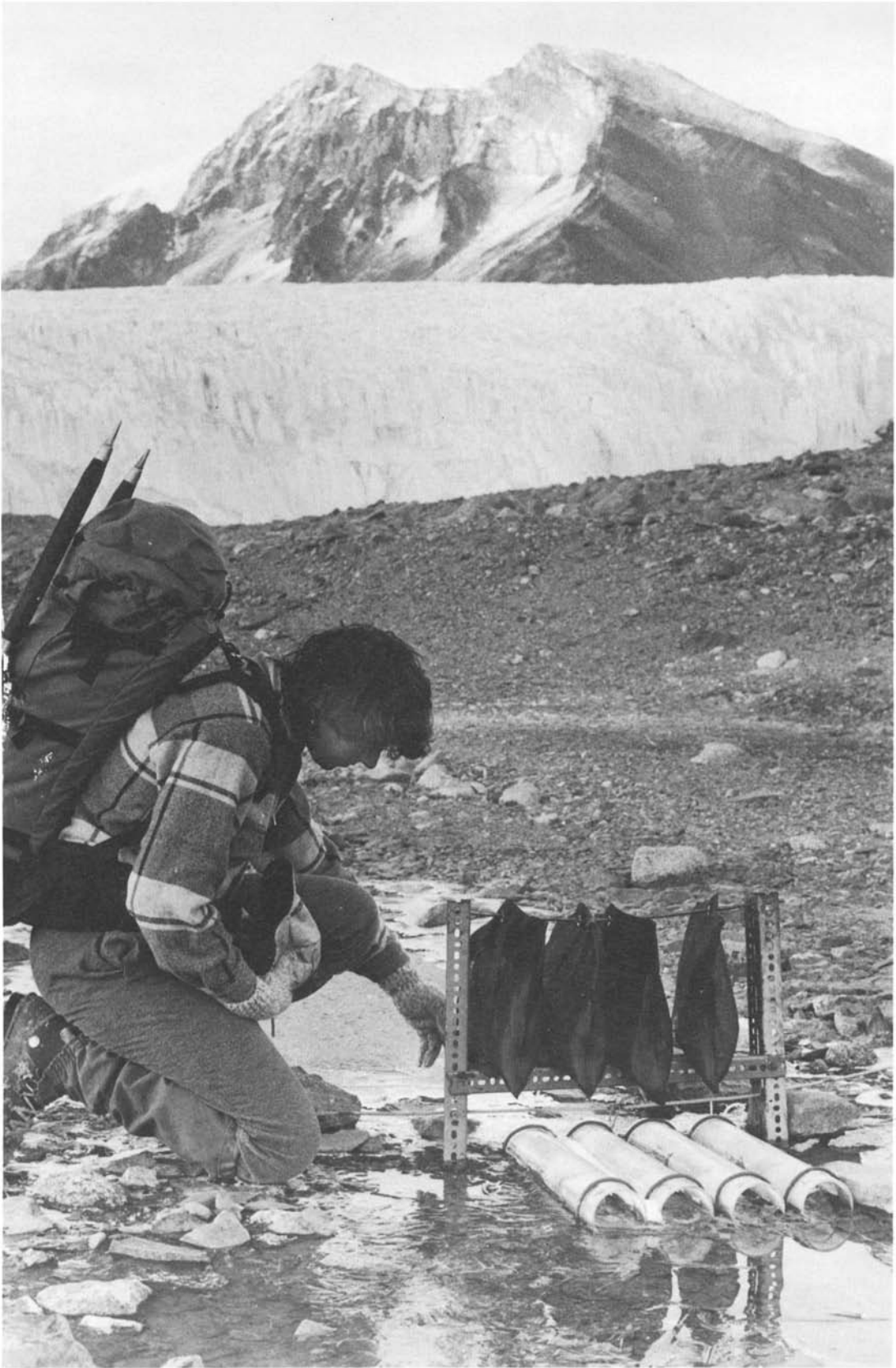


Plate 1. Fryxell stream during early morning low flow conditions showing the nutrient enrichment tubes. The stream water source, the Canada glacier, lies in the background.

tube which delivered a constant flow of 35 ml hr⁻¹ at a 50 cm head. Variability in flow was influenced only by small changes in the reservoir hydrostatic heads as they drained. Reservoirs were topped up every two days and the incubation continued for nine days. Some freezing problems were encountered on days 7, 8 and 9 when the tubes froze briefly in the early hours of the morning. A control tube had stream water only in the reservoir. During tube construction, placing of the mixing baffles was modified relative to Peterson *et al.* (1983) with the aid of dye tracers to ensure an homogeneous mix of added nutrient and stream water by the time it reached 25 cm from the upstream end of the tube. All study samples were placed at this distance in the tubes. Stream discharge and temperatures were monitored several times each day and velocities through the tubes were regularly checked to ensure equal flow through each tube. Communities of *Nostoc*, *Binuclearia* and two *Phormidium* types were subject to the experimental treatments. Initially and at the end of the incubation pigment analyses, N and P tissue concentrations and photosynthetic rates were measured on 3 to 6 replicate samples of each community.

Results

Epilithic biomass

In midsummer, maximum biomass was frequently measured in excess of 15 µg Chl *a* cm⁻² (Table 2). In the low light zone on the underside of the rocks mean maximum values were always high (30–40 µg Chl *a* cm⁻²) but values approaching this could also be found on the exposed upper surfaces of the stream bed in the mats dominated by *Nostoc* and *Phormidium*. A major proportion (20–100%) of this chlorophyll survives the winter in a dry frozen state (Vincent & Howard-Williams, 1986). Some of this may, however, not be photosynthetically active, or even chlorophyll *a* (Vincent & Howard-Williams, 1988).

Standing stocks for three epilithic communities in terms of C, N and P are shown in Table 3. The relatively high inorganic component (silts, sand grains etc) which makes up 60–80% of the dry weight in the *Nostoc* and *Phormidium* mats is reflected by low% C values and hence tissue N and P (Table 3). Carbon as% of dry weight of the mat communities was 5.2 (± SE 0.51) for *Nostoc* and only 1.4 (± SE 0.14) for *Phormidium*. The high inorganic component of the mats probably contributes to considerable light scattering and attenuation within them. The C/N ratio is similar

Table 2. Biomass (µg Chl *a* cm⁻²) of epilithon in three south Victoria Land streams. NF = not found, ND = no data. Values as means (± SD). n ranged from 3–13.

Community	Stream		
	Adams	Fryxell	Onyx
<i>High light</i>			
<i>Nostoc</i> mats and films	27.3 (9.5)	28.0 (9.5)	NF
<i>Gloeocapsa</i> , <i>Schizothrix</i> crusts	11.7		12.0 (18.5)
<i>Phormidium</i> mats			
Pink mats in channels	30.1(17.6)	17.2(10.5)	
Brown furry mats on stones	11.7 (2.6)	1.8 (1.4)	3.0 (2.5)
<i>Crevice</i> s			
<i>Binuclearia tectorum</i> tufts	ND	32.6 (7.3)	NF
<i>Low light</i>			
<i>Prasiola calophylla</i>	32.0 (3.5)	29.6(12.1)	NF

Table 3. Stocks of carbon, nitrogen and phosphorus and N/P ratios in epilithon from Adams and Fryxell streams. Data as mg cm^{-2} , means (\pm SD) ($n > 6$). – = no data.

Community	N	P	C	N/P	C/N
<i>Nostoc</i>	1.8(0.45)	0.13(0.02)	28.1(13.2)	28.1(3.95)	15.6
<i>Phormidium</i>	0.4(0.14)	0.09(0.04)	7.9 (3.2)	4.8 (1.01)	17.5
<i>Binuclearia</i>	1.2(0.28)	0.11(0.04)	–	10.9(0.99)	–

to that reported for antarctic stream chlorophytes (Hawes, 1988) and is high for cyanophyte communities. Perhaps this is because a proportion of the mat is comprised of a polysaccharide matrix (Vincent & Howard-Williams, 1987) and because dead cells are incorporated in this matrix too. The high N/P ratio of *Nostoc* may reflect the N-fixing ability of this community.

Pigment composition and mat structure

The cyanobacterial mats of the high light zone are a complex structure of layers of trichomes embedded in a mucilage (matrix). Associated bacteria (rods and cocci) and a few fungal hyphae have been identified from the matrix (Vincent & Howard-Williams, 1987), and scanning electron micrographs also show fine sediment particles trapped here. Mats in the high light environment produce polysaccharide as the dominant end product of photosynthesis, presumably in part for incorporation into the polysaccharide mat matrix. In the low light, non-mat forming *Prasiola calophylla* community, low molecular weight

compounds were produced as the dominant end product (Vincent & Howard-Williams, 1988).

Light is rapidly attenuated by the mat such that cells in the lower layers of the 0.5–3 mm thick mats are in a low light environment. Those in the upper layers are exposed to bright 24 hr insolation. Photosynthetically active radiation (PAR) is reduced to *ca.* 1% of above surface levels half way through a 9 mm thick *Nostoc* mat, and to 0.01% at the base of the mat. The cells in the lower layers appear to be shade adapted in terms of the amount and composition of their photosynthetic pigments (Table 4). This layer has twice as much chlorophyll *a* on a unit area basis, and when normalised to carbon, a fourfold increase is seen in the lower layers. The phycobilin pigment C-phycocyanin also increased in the bottom layers, but carotenoid accessory pigments were twice as high in the upper portion of the mat. Spectral scans of acetone extracts of the layers (Fig. 1a) clearly show the carotenoid shielding below wavelengths of 500 nm in the mat upper layers and the high chlorophyll peak at 663 nm in the lower layers.

Table 4. PAR and pigment characteristics of the upper and lower layers of an epilithic *Nostoc* mat community, Fryxell Stream. Total mat thickness was 9 mm.

Parameter	Layer		Bottom/Top
	Top	Bottom	
% of mat	63	37	
PAR at base (% of mat surface value)	0.6	0.01	
Chlorophyll <i>a</i> $\mu\text{g cm}^{-2}$	35.4 ± 11.4	74.6 ± 7.3	2.1
Chlorophyll <i>a</i> $\mu\text{g mg C}^{-1}$	4.1 ± 0.7	17.5 ± 2.3	4.3
Carotenoid ratio	4.9 ± 0.2	2.4 ± 0.2	0.5
C-Phycocyanin $\mu\text{g cm}^{-2}$	5.2	15.0	2.9

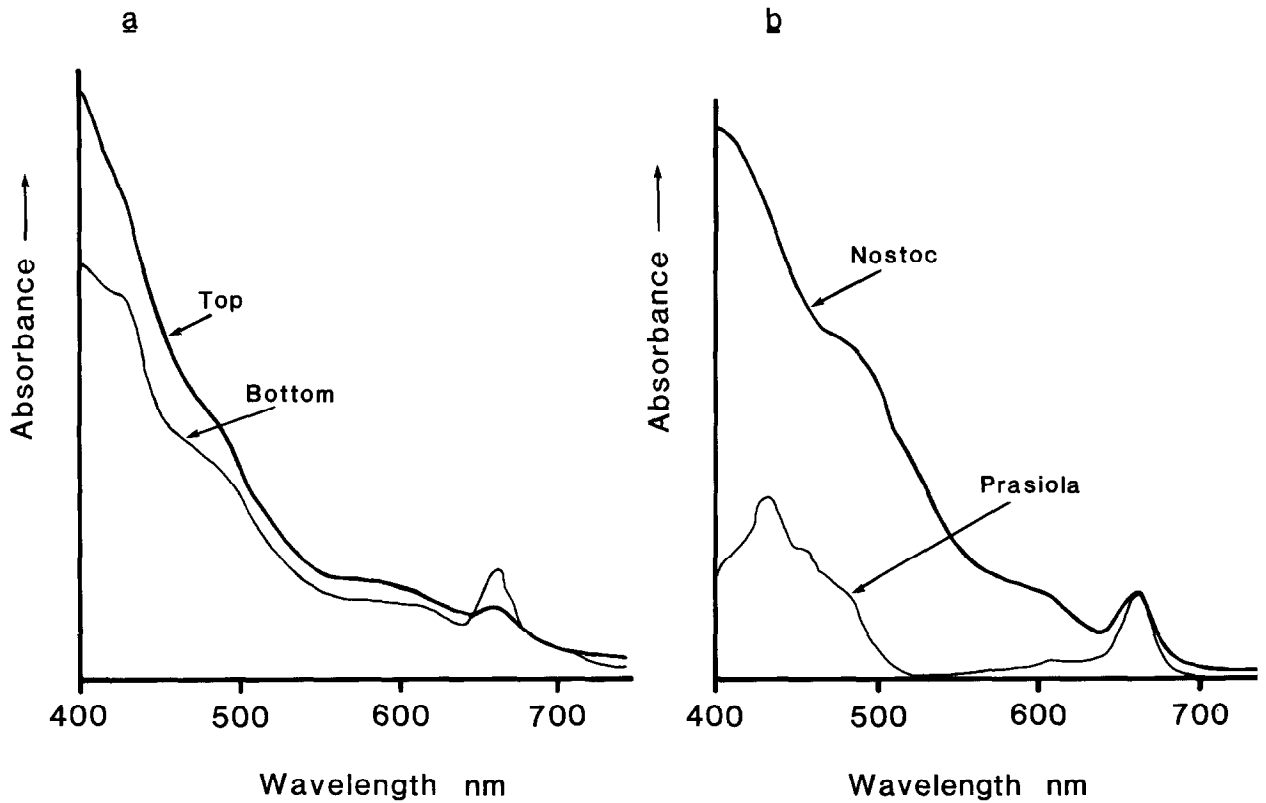


Fig. 1. Absorbance scans of DMSO/acetone extracts of some epilithic communities. (a) Top and bottom sections of a *Nostoc* mat from Fryxell stream. (b) Comparison of a sun (*Nostoc*) and shade (*Prasiola*) community from Adams stream. Data normalised to absorbance at 663 nm.

Distinct differences in pigment composition are seen in the low light habitat community *Prasiola calophylla* when compared with a high light *Nostoc* mat (Fig. 1b). While the spectral scan of the *P. calophylla* community is similar to that for chlorophyll, the scan of *Nostoc* shows a high accessory pigment shielding below 500 nm.

The shade adaptation experiment was run to examine the short term pigment responses to changing light intensity. Within two days of covering a section of the Fryxell stream bed with 95% shade cloth a major increase in chlorophyll *a* was recorded relative to adjacent unshaded control sites (Table 5).

The effect of light intensity on photosynthesis

P vs. I curves for five algal communities comprising four dominant epilithic genera show distinct differences (Figs. 2, 3). Site to site variability in P

vs. I for a given community appears minimal (Fig. 2), as the same response was found for *Nostoc* mats of similar thickness in two very different streams.

However, variability in P vs. I curves between communities is considerable, and follows an expected pattern based on the light regime in the natural habitat (Fig. 3). The shade community,

Table 5. Chlorophyll *a* analyses ($\mu\text{g Chla cm}^{-2}$) on *Phormidium* mats in the sun and shaded with 95% shade cloth over an 8-day period. Data as mean \pm SE for 5 replicate core samples from the mats in Fryxell Stream 6–10 January 1986.

Day	Sun	Shade
0	15.9 \pm 3.1	15.9 \pm 3.1
2	18.1 \pm 3.6	31.8 \pm 5.1
4	17.9 \pm 3.6	28.6 \pm 2.2

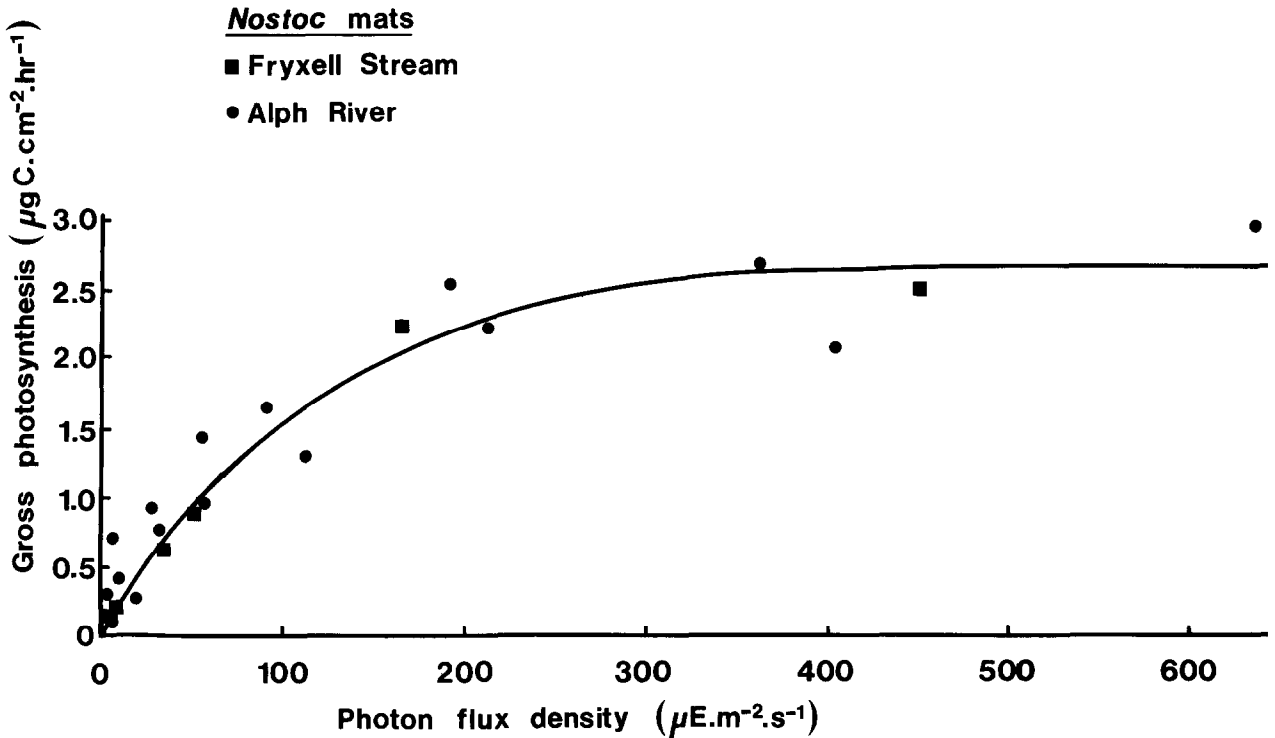


Fig. 2. P vs I relationship for *Nostoc* mats of similar thickness from two streams.

Prasiola, has an I_k value of ca. $20 \mu\text{E m}^{-2} \text{s}^{-1}$, the intermediate light community of rock crevices (*Binuclearia*) and I_k of ca. $70 \mu\text{E m}^{-2} \text{s}^{-1}$, and that for *Phormidium* is ca. $105 \mu\text{E m}^{-2} \text{s}^{-1}$. The highest I_k was found for *Nostoc* and probably results from the high light shielding effect of the dark accessory pigments of this community.

Absolute rates of photosynthesis on a unit area basis increase from sun to shade (Fig. 3) but assimilation numbers ($\mu\text{g C fixed } (\mu\text{g Chl } a)^{-1} \text{ hr}^{-1}$) are higher (0.17) in the sun communities than in the shade (0.09 for *Prasiola*). These assimilation numbers lie well below those recorded for temperate communities. This discrepancy may be due to a proportion of the chlorophyll being in a preserved, non-viable state in these cold conditions. Photoinhibition was not observed in these short-term incubations and we did not detect hysteresis effects when incubations were taken down from bright light to shade.

The effect of nutrients

Nine days of continuous enrichment in the tube experiment (Plate 1) had surprisingly little effect on three test epilithic communities (Table 6). Fryxell stream was chosen for this study as the ambient nutrient levels were lower than those recorded in other Victoria Land streams (Table 1) (Howard-Williams *et al.*, 1986b). During the incubation period ambient stream inorganic nitrogen levels ranged from 3.6 to 6.1 mg m^{-3} of $\text{NO}_3\text{-N}$ and 1.9 to 7.0 mg m^{-3} $\text{NH}_4\text{-N}$. DRP varied between 1.3 and 2.0 mg m^{-3} . Enrichment of the tubes was calculated to increase the $\text{NO}_3\text{-N}$ to 200 mg m^{-3} and the DRP to 20 mg m^{-3} . Spot checks were carried out twice during the incubation by sampling the outflow ends of the tubes. The mean DRP value in the +P treatment was 23.6 mg m^{-3} , the $\text{NO}_3\text{-N}$ in the +N treatment was 186 mg m^{-3} and in the N + P treatment DRP and $\text{NO}_3\text{-N}$ were 36.0 and 262 mg m^{-3} .

A positive response in terms of tissue nitrogen

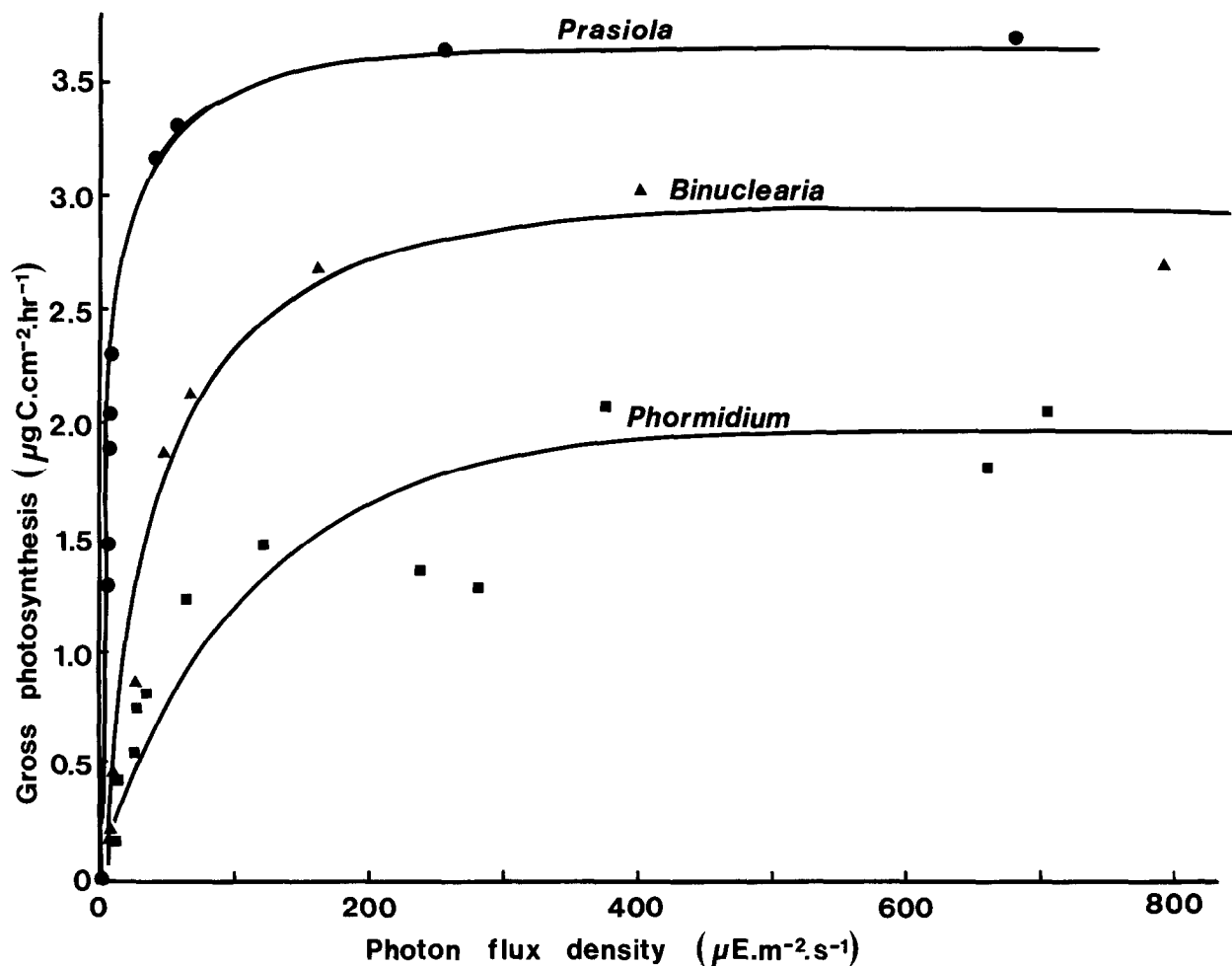


Fig. 3. P vs I relationships for a sun (*Phormidium*), shade (*Prasiola*) and intermediate light (*Binuclearia*) community.

and chlorophyll *a* was shown by *Binuclearia* in the +N enrichment, and tissue phosphorus in all three communities increased significantly ($P < 0.05$) in the N + P treatments. However, of note is that the N/P ratio in the tissues declined significantly ($P < 0.01$) in *Nostoc* in the +P and N + P treatments (Table 6). Neither *Nostoc* nor *Phormidium* mats showed any biomass response to enrichment. However, as we were examining changes in an established community, comparison with other studies (e.g. Peterson *et al.*, 1983; Hullar & Vestal, 1988) which measured colonisation of new substrates, is difficult.

There was no response to enrichment in terms of community photosynthetic rates (Table 6) and

F values in one-way analyses of variance were all less than F at $P = 0.05$. It would appear therefore that nutrient levels in Fryxell stream do not limit either biomass accumulation or photosynthetic rates of the epilithic communities. The continuous supply of nutrients by the stream water with a mean velocity of $0.26 \text{ m}^{-3} \text{ s}^{-1}$ through the tubes was adequate for growth.

Discussion

Photosynthetic rates of epilithon for a variety of streams are described in the review by Lock (1981). A range of mean values (from a mixture of

Table 6. Response of three communities to 9 days of continuous enrichment with nitrogen (+ N), phosphorus (+ P) and N + P combined. Controls (C) had no enrichment. Data as means \pm SE. Significant ($P < 0.05$) responses above (or in the case of N/P ratios, below) control values are indicated with an asterisk.

Measurement		Species					
		Binuclearia		Phormidium		Nostoc	
		x	(\pm SE)	x	(\pm SE)	x	(\pm SE)
Chlorophyll <i>a</i> $\mu\text{g cm}^{-2}$	C	27.4	(3.02)	17.2	(1.96)	28.0	(1.71)
	+ P	21.9	(2.76)	9.1	(0.71)	11.8	(1.14)
	+ N	39.7*	(3.62)	9.2	(0.69)	28.3	(4.18)
	+ NP	26.2	(2.75)	12.2	(2.37)	25.7	(3.98)
Gross Photosynthesis $\mu\text{g C cm}^{-2} \text{ hr}^{-1}$	C	2.64	(0.28)	1.58	(0.47)	1.10	(0.64)
	+ P	1.56	(0.30)	1.94	(0.32)	1.64	(0.43)
	+ N	1.42	(0.12)	1.94	(0.17)	2.16	(0.21)
	+ NP	2.26	(0.37)	1.60	(0.09)	1.25	(0.07)
Microbial Phosphorus $\mu\text{g g}^{-1}$	C	1.72	(0.01)	0.74	(0.01)	1.01	(0.06)
	+ P	2.30	(0.17)	0.77	(0.01)	1.15	(0.04)
	+ N	2.52	(0.07)	0.81	(0.03)	0.99	(0.04)
	+ NP	4.10*	(0.53)	1.15*	(0.03)	1.56*	(0.06)
Microbial Nitrogen $\mu\text{g g}^{-1}$	C	18.9	(0.17)	3.2	(0.24)	12.4	(1.13)
	+ P	21.2	(1.13)	3.8	(0.05)	11.1	(0.40)
	+ N	27.8*	(0.06)	3.5	(0.30)	12.1	(0.68)
	+ NP	21.4	(0.29)	3.8	(0.14)	10.4	(0.14)
N/P ratio	C	10.98	(0.16)	4.32	(0.38)	12.16	(0.39)
	+ P	9.21	(1.18)	4.94	(0.01)	9.65*	(0.04)
	+ N	11.03	(0.36)	4.32	(0.23)	12.22	(0.22)
	+ NP	5.21*	(0.65)	3.30	(0.02)	6.66*	(0.31)

net and gross photosynthesis measurements) from 0.8 to 11.3 $\mu\text{g C cm}^{-2} \text{ hr}^{-1}$ is reported. In a North American desert thermal stream colonised by cyanobacterial mats Naiman (1976) found production rates of ca. 29 $\mu\text{g C cm}^{-2} \text{ hr}^{-1}$. Area based P_{max} values for the Victoria Land stream communities reported here (Figs. 3, 4) vary from 2.0–3.6 $\mu\text{g C cm}^{-2} \text{ hr}^{-1}$ are within, but are at the lower end of, the range for temperate communities. However, assimilation numbers of less than 0.2 $\mu\text{g C} (\mu\text{g Chl}a)^{-1} \text{ hr}^{-1}$ are much lower than those of temperate communities. During stream flow in the short summer of this region PAR varies between 1000 $\mu\text{E m}^{-2} \text{ s}^{-1}$ at midday and 100 $\mu\text{E m}^{-2} \text{ s}^{-1}$ at midnight. Reference to Figs. 2 and 3 shows that the sun communities operate for 24

hours in a diel regime of PAR in which light limitation to photosynthetic rates does not occur. As light is unlikely to be a control on photosynthesis in these communities the relatively low I_k values (ca. 100 $\mu\text{E m}^{-2} \text{ s}^{-1}$) are of interest.

Goldman *et al.* (1972) showed a marked midday depression in photosynthetic rates of benthic algal mats in ponds at Cape Evans, Ross Island at the same latitude as Fryxell stream. They attributed this to marked photoinhibition during this time of day with maximum photosynthetic rates occurring close to midnight on bright days. The light shielding effect of the accessory pigments in the upper layers of the mats of the high light stream communities (Fig. 1, Table 4) thus appears to have the effect of reducing the I_k of the community as the bulk of the

chlorophyll is found in the lower layers. High carotenoid/chlorophyll *a* ratios in antarctic lake benthic algal felts has been suggested to be due to chlorophyll degradation in the high light rather than a carotenoid buildup (Goldman *et al.*, 1963). Layering and high carotenoid pigment levels were not observed in the low light community (*Prasiola*) which exhibited a very low I_k value (Fig. 3) and even in this community we did not detect photo-inhibition. Given the saturation values and the absence of photoinhibiting effect we would expect saturated photosynthesis to operate throughout the 24 hour cycle. It is puzzling that the shade adapted *Prasiola* community did not show photoinhibition and it is of interest that another antarctic low light and temperature community (*Trachyneis aspersa*) also has this property (Palmisano *et al.*, 1985).

Peterson *et al.* (1983) point out that information on the response of stream periphyton to nutrient enrichment is scarce as streams are difficult to treat experimentally. However, studies on temperate and arctic streams have indicated that in non-shaded conditions, the supply of N and/or P to algal mats could limit photosynthesis (Peterson *et al.*, 1983; Triska *et al.*, 1983; Hullar & Vestal, 1988).

Lock & John (1979) suggest that at low concentrations nutrient uptake by stream periphyton may be limited by diffusion because of laminar boundary layers over the biofilm. This effect is likely to be enhanced by the presence of the polysaccharide matrix surrounding the cells (Vincent & Howard-Williams, 1987). Where diffusion limitation occurs the concentration of nutrients in the stream water would be the critical factor, even though the supply is continuous. Hence the findings of Wuhrmann & Eichenberger (1975) that enrichment of an unshaded Swiss stream resulted in no increase in periphyton growth may be explained by relatively high concentrations of DRP (78 mg m^{-3}) and $\text{NO}_3\text{-N}$ ($> 500 \text{ mg m}^{-3}$) in the ambient stream water. In deep shade, where light is a primary control, nutrients were found to be unimportant even where nitrate levels were undetectable in summer months (Triska *et al.*, 1983). The benthic algal felts of the ponds of Cape

Evans, however, showed no enhanced photosynthesis on the addition of inorganic N, P or trace elements (Goldman *et al.*, 1972) in high light conditions. Although these authors concluded that nutrients did not limit benthic algal photosynthesis in the ponds, the incubations were of short duration (4 hrs) and the ponds were nutrient rich due to Antarctic skua (*Catharacta mac-cormicki*) bathing activities here. Vincent & Vincent (1982) also recorded no nutrient limitation of phytoplankton of ponds along the edge of the Ross Sea, and similarly attributed this lack of response to the high natural nutrient levels here. Hawes (1988) has shown that in maritime Antarctic Signy Island, the chlorophyte *Klebsormidium* sp. was significantly associated with streams of high dissolved phosphorus content. He was careful to emphasise, however, that other, particularly physical factors may also have been of importance in determining the distribution of this species.

Our data from low nutrient Fryxell stream consistently showed no response in photosynthetic rates or chlorophyll *a* to nutrient enrichment after 9 days. Even in *Binuclearia* and *Nostoc* where a response in terms of increased tissue phosphorus occurred which significantly reduced the N/P ratio (Table 6), this enhanced nutrient status was not translated to growth. We assume that the phosphorus uptake was a luxury response. A similar effect was reported by Wuhrmann & Eichenberger (1975) where, in their stream treatments with P, the tissue N/P ratio decreased due to luxury uptake of P but no response to algal growth was recorded.

While we have identified the primary controls of epilithic biomass in the Victoria Land streams as bed stability and sediment load (Vincent & Howard-Williams, 1986; Howard-Williams *et al.*, 1986b), the explanation of the low photosynthetic rates clearly does not lie with light or nutrients. In this way these streams differ from their temperate and even arctic counterparts where light and/or nutrients (Triska *et al.*, 1983; Peterson *et al.*, 1983; Elwood *et al.*, 1981; Hullar & Vestal, 1988) and even space (Matson & Klotz, 1983) control lotic primary production. The absence of light or

nutrient limitations in south Victoria Land streams further emphasises the need to consider other potential controls on plant growth here.

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