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EFFECTS OF NATURAL UV RADIATION ON ANTARCTIC CYANOBACTERIAL MATS

Antonio QUESADA[1], Lynda GOFF[2] and Deneb KARENTZ[3]

[1] *Departamento de Biología, Universidad Autónoma de Madrid, 28049 Madrid, Spain*
[2] *Department of Biology, University of California, Santa Cruz, California 95064, U.S.A.*
[3] *Department of Biology, University of San Francisco, San Francisco, California 94117-1080, U.S.A.*

Abstract: Microbial mats dominated by cyanobacteria are the most abundant living forms in non-oceanic Antarctic ecosystems. The ultraviolet radiation increase may affect drastically the organisms living in the polar regions and especially those of terrestrial ecosystems exposed to full sunshine. The aim of this work was to investigate the effect of UV radiation on terrestrial Antarctic communities.

Dominant species in these microbial assemblages belonged to the filamentous, non-heterocystous cyanobacteria group (*e.g. Phormidium*, *Lyngbya*, *Oscillatoria*, etc). Heterocystous (*e.g. Nodularia*) and coccoid (*e.g. Synechococcus*) cyanobacteria were subdominant although very abundant. We studied the effect of natural UV radiation on cyanobacterial mats, using a series of narrow band UV filters. After two weeks of differential exposure to UV (PAR, PAR+UVA, PAR+UVB, PAR+UVA+UVB) population structure, pigment composition and physiological activities were analyzed.

Although statistical analyses revealed that mats under the four UV regimes assayed were not significantly different in community structure nor in pigment composition, surface appearance of mats was different between treatments. Physiological analyses indicated that the photosynthesis/respiration balance might be affected by UV radiation.

The apparent contradiction between analytical data of pigments and surface appearance can be explained by considering that UV regime might have induced changes in the position of the microrganisms of the mat by mean of migration. This process is suggested to be one of the responses of escaping from an increasing UVB radiation environment.

key words: Antarctica, cyanobacteria, McMurdo Sound, mycosporine-like-aminoacids, UVB

Introduction

Microbial communities involving cyanobacteria dominate terrestrial and freshwater polar ecosystems (*e.g.* VINCENT and QUESADA, 1994). These communities have been studied from the taxonomic point of view (BROADY and KIBBLEWHITE, 1991), but their physiology and ecology have been scarcely investigated *in situ*.

Ultraviolet-B (UVB: 280–320 nm) radiation reaching the Earth's surface has

increased during the past 2 decades as a consequence of the ozone depletion in the upper atmosphere (CRUTZEN, 1992). UVB is a harmful component of the solar spectrum for the living beings with a variety of effects. The main targets of UVB radiation include DNA (CALDWELL, 1979), several proteins (enzymes and membrane carriers; *e.g.* KRAMER *et al.*, 1992; DÖHLER *et al.*, 1991), the photosynthetic apparatus (FRISO *et al.*, 1994), RUBISCO (WILSON *et al.*, 1995), etc. Photosynthetic organisms are specially sensitive to UVB due to the UVR absorbing capabilities of some components. However, strategies to avoid or to reduce UVB damages are present in many kinds of organisms (MITCHELL and KARENTZ, 1993). Some species produce UVB absorbing pigments (flavonoids, mycosporine-like amino acids) that screen UVB from the sensitive cellular fractions; another strategy is to avoid the impact of UVB by escaping to habitats with reduced UVB intensity (deeper in the water column or in the mat structure; *e.g.* GARCIA-PICHEL *et al.*, 1993); organisms may produce quenching agents that reduce the toxic effects of the superoxide produced by UV radiation (UVR) exposure; and finally a variety of repair mechanisms allow the reconstruction of the damaged structures (FRIEDBERG, 1985).

Recently, extensive literature on UVB effects on different organisms has become available; however, most of the published results have been undertaken in laboratory, with artificial PAR and UV sources, and with isolated organisms. QUESADA *et al.* (1995) have suggested that the balance between PAR/UVA/UVB may be a most significant factor in the efficiency of damage/repair mechanisms. Therefore, results obtained in laboratory experiments with single UV sources (unbalanced spectra) may not represent completely the physiological and ecological effects of natural UVB exposure.

The aim of this study was to analyze the effects of natural UV radiation on undisturbed cyanobacterial mats in Antarctica, comparing their response to different wavelength bands. We investigated the physiological (photosynthesis and respiration) adaptations to the different UV regimes and the variation of pigment concentration and UV screening compounds.

Material and Methods

Sampling was conducted during austral summer 1996 (January and February) in Casten Pond, located on the McMurdo Ice Shelf ablation zone (78°S, 166°E) close to Bratina Island. This area is an extensive region dotted with ponds of different chemical and biological characteristics (see HOWARD-WILLIAMS *et al.*, 1989). Environmental measurements, of pH, dissolved oxygen and conductivity were taken at the sampling periods. Water temperature was recorded continuously at three different depths (surface, 5 and 15 cm bellow surface) within the water column (several meters inside the lake). Radiation data were provided by Biospherical Instrument Inc. from the National Science Foundation Polar Programs UV Radiation Monitoring Network.

The experiments on UV radiation were undertaken *in situ* using a series of filters mounted adjacent to each other on a 60 cm by 15 cm UV transparent acrylic sheet (Plexiglass UVT, Rohm Haas). These filters, cut in squares of 15 by 15 cm, were: Acrylite OP3 (Cryo), which is UV opaque and does not allow any UVR coming through; Mylar D (Dupont), which cuts all the UVB radiation; a chemical filter made of a solution of

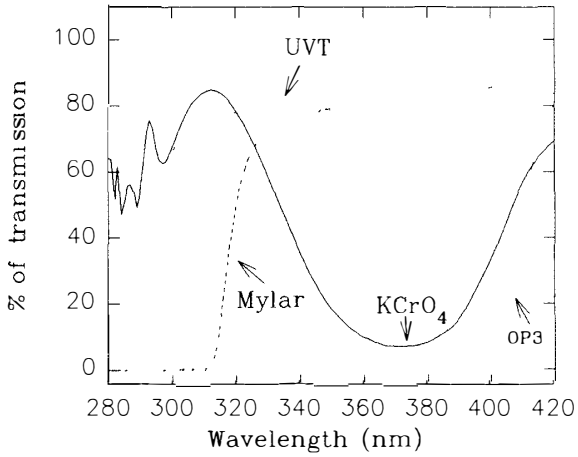

Fig 1 Absorption spectra of the filters used in the experiments

50 mg l^{-1} $KCrO_4$ inside a polyethylene (Whirlpak) bag, this filter absorbs UVA and allows *ca.* 70% of UVB to pass through; or a second layer of plexyglass UVT. Optical properties of each filter are shown in Fig. 1.

Four replicates of each filter set were installed *in situ* above a homogeneous layer of cyanobacterial mat. At three time intervals: 0, 6 and 11 days, square portions of mat under each filter were taken, with plastic wide spatula (mat was firm enough not to disturb the microorganisms distribution with sampling), stored in the shade until transportation by helicopter to McMurdo Station (within 3–4 hours from samples collection). Cores of 12 mm diameter were taken from each sample. Immediately physiological activities (^{14}C uptake and photosynthesis *versus* irradiance curves) were measured. The remaining cores were frozen at −20°C until pigment extractions were made. From each filter set, 3 cores from each treatment were used for each determination.

One way ANOVA was used to test statistical significance of the differences between the treatments.

Pigment extraction and determination

Chlorophyll *a* (Chl *a*) and carotenoid concentrations were measured following acetone extraction. Sample cores were sonicated in 90% acetone (HPLC grade) and then extracted overnight in darkness at 4°C . The extracts were centrifuged at *ca.* 12000 g for 10 min and absorbance scans were undertaken with diode array spectrophotometer (Beckman model 640). This procedure was repeated on the same pellet until no more pigment was extracted, usually three times were necessary. Chl *a* concentration was determined using the extinction coefficient of Marker (MARKER *et al.*, 1980) adding the concentration of the three extractions. Total carotenoid concentration was estimated from the same scans (acetone extracts) reading at 475 nm (BRITTON, 1985).

Reverse-phase HPLC separation of hydrophobic pigments was done using the methodology of VINCENT *et al.* (1993b). A Hewlett-Packard system (model 1050), provided with a fluorescence detector (Hewlett-Packard model 1046A) set at 430 nm excitation and 665 nm emission and a UV diode array detector (Hewlett-Packard) set at 440 nm, was used. Peak identification was done by comparison with published chromatogram obtained using the same methodology and similar biological material (VINCENT *et al.*, 1993b). Absorption spectra with every isolated peak from the chro-

matogram also corroborated the identification of some of the compounds.

Phycobiliproteins in mats were extracted using the osmotic shock technique (WYMAN and FAY, 1986). Cores were immersed in glycerol and sonicated until a paste was produced, and incubated under these conditions for 2 hours at 4°C in darkness. After this period 10 volumes of distilled water were added and shaken vigorously. Then extracts were centrifuged at 12000 *g* for 10 min and absorption scans of supernatants were made. The procedure was repeated three times on the same pellet. Phycobiliprotein concentration was estimated using the equations of BENNET and BOGORAD (1976).

Determination of UV absorbing compounds (mycosporine-like amino acids [MAA])

UV absorbing pigments were extracted from cores after sonication of these in 20% (v/v) aqueous methanol maintained at 45°C for one hour, according to the method of GARCIA-PICHEL and CASTENHOLZ (1993). After this time, extracts were centrifuged at 12000 *g* for 10 min and the supernatant scanned. This procedure was repeated three times to ensure that all the UV absorbing compounds were extracted. The relative concentration was evaluated from the absorbance of the UV peak (334 nm). The methanolic extracts were also separated by HPLC (Waters), and detected by photodiode array (Waters, 991), following the method of Karentz (KARENTZ *et al.*, 1991) based in DUNLAP *et al.* (1986). The retention times and absolute concentration of each compound were calibrated with known standards.

Determination of physiological activities

Photosynthesis was evaluated as ^{14}C uptake, in whole cores. The cores were placed outdoors in Whirlpak bags with the same temperature that they had in Casten Pond at the sampling moment. Cores were incubated in triplicates under the same set of filters used during the differential exposure *in situ*. Two m*l* of TRIS buffer (pH 8) containing 2 μCi of ^{14}C (as sodium bicarbonate) were added to each bag, taking care that the cores were completely immersed in the radiolabeled solution. The incubation lasted for 2 hours, afterwards bags were immediately frozen in solid CO_2 and kept in the dark until analyses were completed. Sample preparation consisted in sonication of cores (after thawing) in 1 m*l* of TRIS buffer (pH 8). 0.2 m*l* aliquots were placed in 7 m*l* scintillation vials, and acidified with 0.1 m*l* of 50% acetic acid in order to eliminate the radiolabeled bicarbonate non incorporated. All the previous processes were run in darkness. Scintillation vials were dried and 5 m*l* of scintillation liquid (Ecolume, ICN) were added to the vials and counted in scintillation counter (Beckman LS 6800). Results are expressed in relative unit (dpm).

Balance photosynthesis-respiration in intact cores was analyzed by mean of the Photosynthesis *versus* Irradiance (P *vs* I) curves made on oxygen evolution basis, using Illuminova (Illuminova, AB. Uppsala, Sweden). This apparatus consists of an integrated set of oxygen microelectrode immersed in a temperature controlled cuvette, and a computer controlled PAR source. Oxygen measurements were done immediately after transportation of samples from the field station, meanwhile cores were maintained at *ca.* 2°C in darkness. The core was placed in the 3 m*l* chamber with the mat surface facing the light source. A 40 min program was used, with 9 light intensities for 4 min each one. Light intensities were: 0, 8.9, 25.3, 41.7, 74.5, 115.8, 239, 485.5, 813.9 and 0

again (in μmol photon $m^{-2} s^{-1}$). The rate of oxygen evolution was integrated as mmol $O_2 cm^{-2} h^{-1}$. Maximal photosynthesis (P_{max}) and the slope of the light limited portion of the curve (α), were calculated using the Webb model (WEBB *et al.*, 1974).

Results

Environmental characteristics

The experimental mat in Casten Pond (about 100 m long, 50 m wide, depth was not measured but estimated lower than 3 m) was homogeneous and covered most of the lake bottom. In the chosen sample area the water was 10–15 cm deep (changes in the water level were observed) and the mat was 2–3 mm thick, with brown color on the surface and blue-green color underneath. Separation into different layers was not possible by mechanical procedures. Casten Pond showed moderate conductivity ranging from 1500 to 1800 $\mu S cm^{-1}$ during the experimental period. pH was always alkaline, *ca.* 9.6, although it was measured only during the apparent day (from 1000 to 1600 local time). Oxygen concentration in water was always slightly lower than the saturation values, ranging between 80 and 95%. Water temperature varied between 1.8 and 8°C, although some mornings ice was present on the shores. Although water chemistry variables were not measured in 1996, this pond and the area in general is considered limited by N since P reaches high concentrations (HAWES, 1996; personal communication). During the experimental period, radiation was measured at McMurdo Station in three bands: PAR which ranged between 200 and 1350 μmol photon $m^{-2} s^{-1}$; UVB with average value of 66 $\mu W cm^{-2}$ (n = 173) and minimum and maximum values of 6 and 174 $\mu W cm^{-2}$ respectively; and UVA radiation averaged 1948 $\mu W cm^{-2}$ (n = 173) and minimum and maximum irradiance were 375.7 and 4265 $\mu W cm^{-2}$ respectively.

Visual results

After the exposure to different UV conditions, the mats presented a color gradient. The mat exposed only to PAR (OP3 filter) was more pigmented (more deep green) than the other mats. Cyanobacteria exposed to all the solar wavelengths (UVT filter) and UVB and PAR ($KCrO_4$ filter) were less pigmented. PAR plus UVA (Mylar filter) produced an intermediate pigmentation.

Community structure

The taxa dominating the mat community belonged to the Cyanophyta group, although other primary producers as diatoms and green algae were scarcely found. The matrix of the mat consisted of a very thin (aprox. 1 μm thick) cyanobacteria classified as *Lyngbya* sp. However, this community was very diverse and many other taxa were found. *Nodularia* sp. and *Anabaena* sp. were especially abundant and were considered as subdominant. Filaments of both of these cyanobacteria frequently contained heterocysts. Other cyanobacteria present, but not in large numbers, were a fast gliding *Oscillatoria* sp. with filaments 10 μm wide, *Phormidium* sp. (3.5 μm wide) and a picocyanobacteria *Synechococcus* sp. Some filaments of the *Oscillatoria* sp. showed a very intense red color that was not due to phycoerythrin, since it did not fluoresce under green excitation.

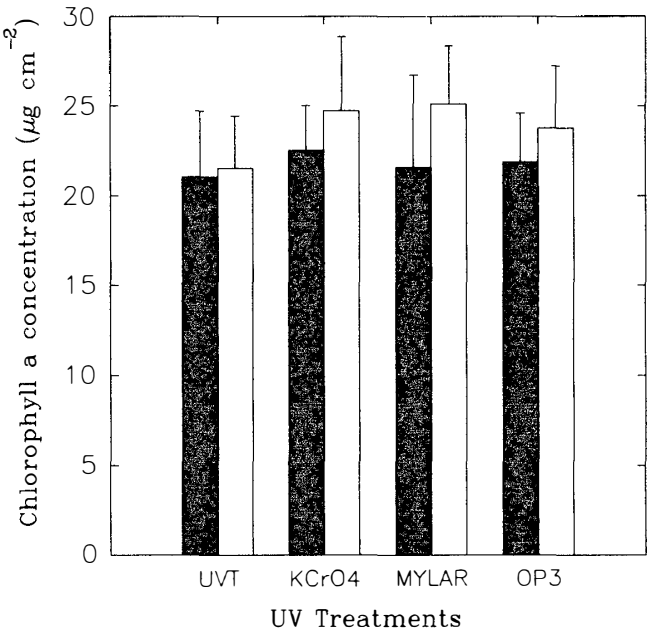

Fig. 2. Chlorophyll *a* concentration obtained from cores under the 4 UV treatments after 6 (solid bars), and 11 (hollow bar) days. UVT represents the cores under the full solar spectrum (UVT filter), $KCrO_4$ represents the cells exposed to PAR and UVB (no UVA), Mylar indicates the mats under PAR and UVA (no UVB), and OP3 shows the results of mats under just PAR (no UVA, no UVB). Error bar is the standard error.

Microscopic observation of three samples from each light treatment after 6 and 11 days of exposure showed no apparent qualitative differences in taxonomic structure in semi-quantitative analysis.

Pigment characteristics

Over the 11-day study period Chl *a* concentration in cores from the mats under the different light treatments, increased slightly (on average 9.2%). Although data showed lower values under the UVT filter (Fig. 2) differences between treatments were not significant (ANOVA one way) neither in the first nor in the second sampling period.

Carotenoids (Car) concentration showed the same trends as Chl *a* (Fig. 3), with lower values under UVT treatment. The ratio Car/Chl *a*, which may indicate a shift in the photosystem structure, showed very constant values under the different treatments in both sampling periods (Fig. 4).

HPLC separation of acetone extracts allowed us to identify 7 pigment compounds that were present in every sample (Table 1). The occurrence of these compounds was determined by comparison with previously published chromatograms and with the shape of the absorption spectra could be identified as: myxoxanthophyll (retention time = 8.62 min), P6D1 (rt = 9.14 min), M2 (rt = 9.7 min), canthaxanthin (rt = 11.92 min), Chl *a* (rt = 13.37 min, validated with standards), echinenone (rt = 14.14 min) and *β*-carotene (rt = 18.27 min). VINCENT *et al.* (1993b) suggested that P6D1 and M2 might be forms of canthaxanthin and myxoxanthophyll respectively. Although the area under the peak changed with time and with light treatment, the pigment results indicated that there is not a clear trend in the relative composition of carotenoids under the various exposures.

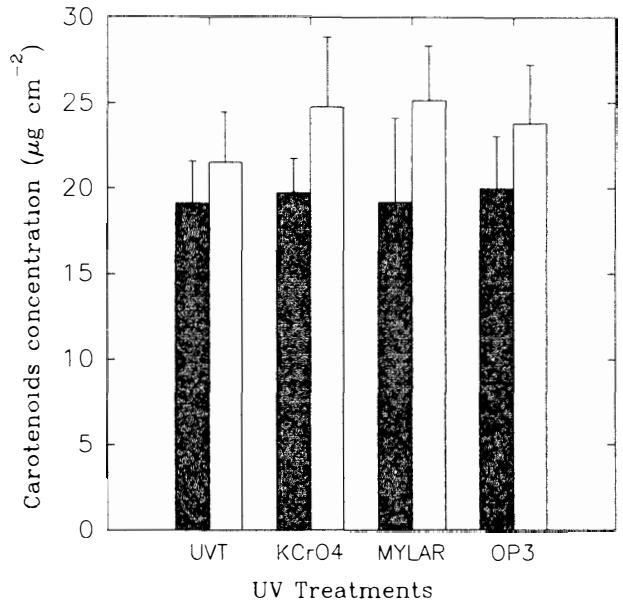

Fig 3 Carotenoids concentration obtained from cores under the 4 UV treatments after 6 (solid bars), and 11 (hollow bar) days. Legends as in Fig. 2

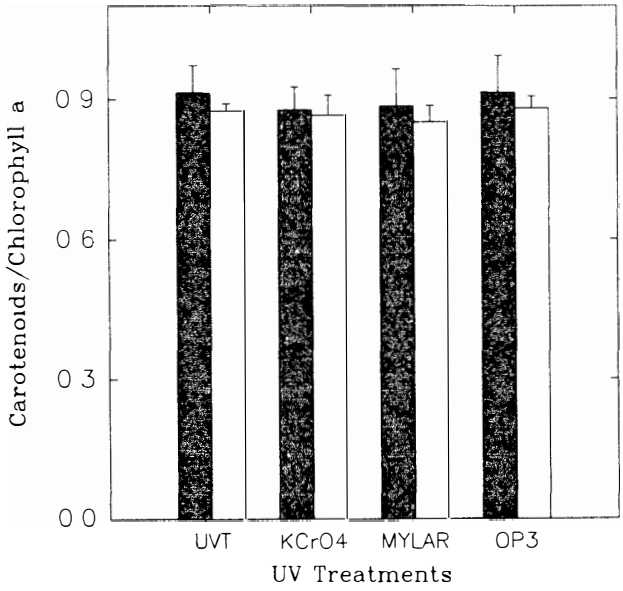

Fig 4 Carotenoids/Chlorophyll *a* ratio (in concentration) from cores under the 4 UV treatments after 6 (solid bars), and 11 (hollow bar) days Legends as in Fig. 2

Higher number of chromatograms are needed to identify any statistical trend.

The phycobiliproteins (PBP) phycocyanin (PC) and phycoerythrin (PE) were identified from their absorption and fluorescence characteristics (data not shown). PC was more abundant and represented 80% of the total PBP. Thus, results will be shown as a function of PC (Fig. 5). As variations of the extractive technique were applied on samples from the first and the second week, comparisons between PBP concentration in both periods cannot be made. On average PC concentration was lower under UVT

Table 1. HPLC separation of the acetone extraction from cores of cyanobacterial mats. Units are the area under the peaks.

Treatment	UVA	UVB	Pigments						
			Myxoxan	P6D1	M2	Canthax	Chl *a*	Echinen	β-Carotene
UVT	+	+	239.5	53.6	75.9	309.2	412.1	112.6	116.9
MYLAR	+	−	249.2	85.5	75.1	409.8	643.5	378.1	162
OP3	−	−	259.5	142.8	71.8	473.5	474.2	309.5	120.2
$KCrO_4$	−	+	303.5	179	201.3	502.5	530.4	336.2	113.9

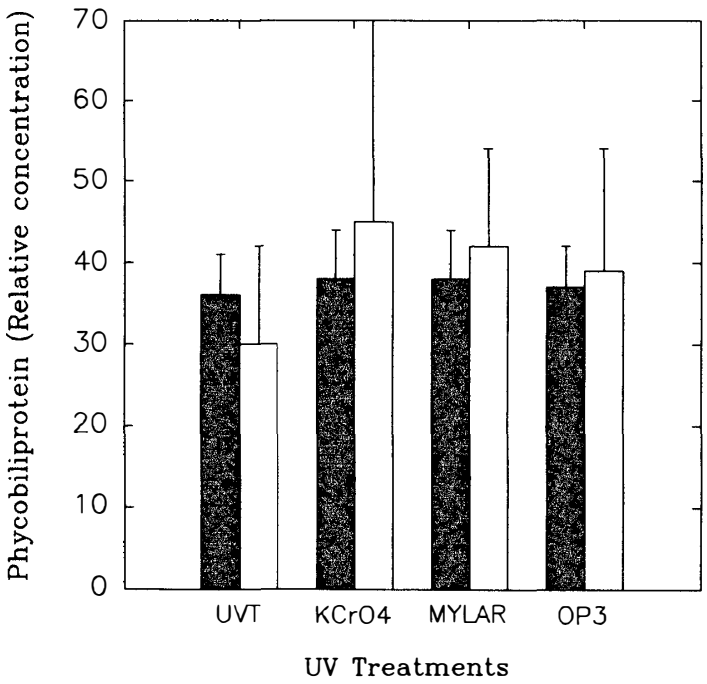

Fig. 5. Phycobiliproteins concentration obtained from cores under the 4 UV treatments after 6 (solid bars), and 11 (hollow bar) days. Legends as in Fig. 2. Data in relative concentration since extractive technique was slightly different in the first and second weeks.

treatment (Fig. 5) although differences were not significant (ANOVA one way, repeated measurements). The rest of the treatments showed similar mean values. PBP concentration expressed in Chl *a* basis showed very similar trends.

UV absorbing compounds

The absorption spectrum of the methanol extraction showed that a well marked absorption peak occurs in the 340 nm region (Fig. 6). HPLC separation of the methanolic extracts (Fig. 7) shows a distinct peak which was identified as the MAA porphyra-334. The occurrence of this compound was constant through the experimental period and no other major peaks appeared. The compared absorbance of this compound, showed in Fig. 7, indicated that porphyra-334 concentration decreased slightly over the study period, although differences between treatments were not significant. Similar trends

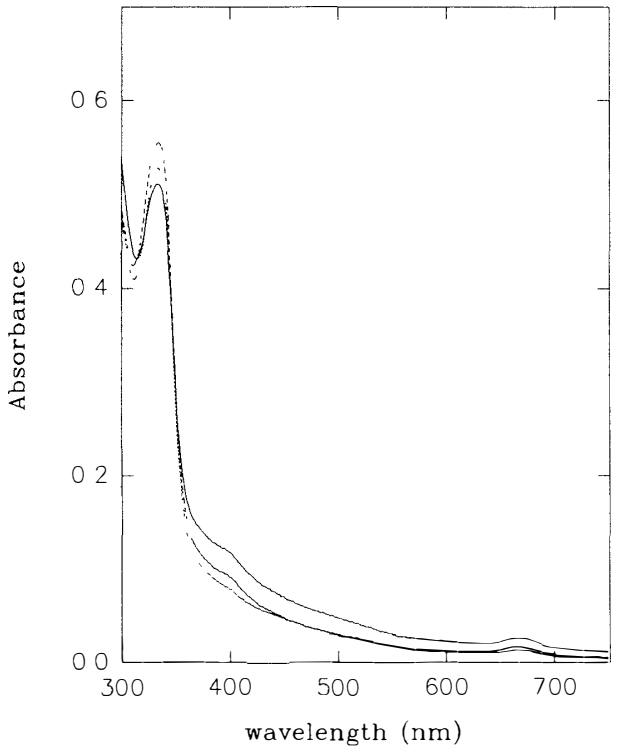

Fig 6 Absorption spectrum of methanolic extraction showing the UV absorbing compound The three lines represent the three replicates of the treatment

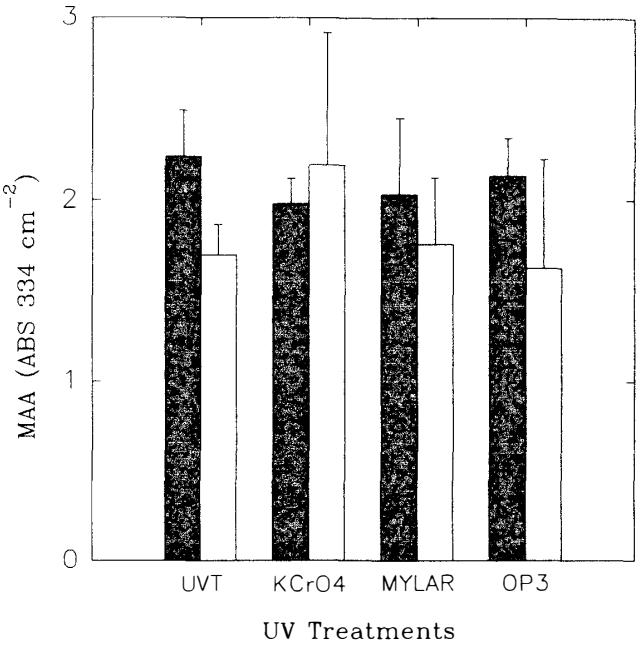

Fig. 7. MAA (porphyra-334) concentration obtained from cores under the 4 UV treatments after 6 (solid bars), and 11 (hollow bar) days. Legends as in Fig 2.

were found when results are expressed in Chl *a* basis.

Physiological characterization

^{14}C uptake data showed that on average (four replicates from each treatment after 6 days of exposure) mats exposed to the whole UV spectrum had 25% lower photosynthesis than cells under just PAR (Fig. 8), although the differences were not significant, because of the high standard deviation between replicates of treatments.

In the P-I curves, alpha (α) values were maximum under the full UV environment (UVT; Table 2). In the other light treatments α values were consistently 50% of the α value under UVT. Maximum O_2 production rate (P_{max}) followed similar trends. Mats under UVT exposure showed the maximum value while the rest of the treatments exhibited lower values. Photosynthesis-respiration balance can be studied from these results by analyzing the compensation point which indicates the light intensity at which

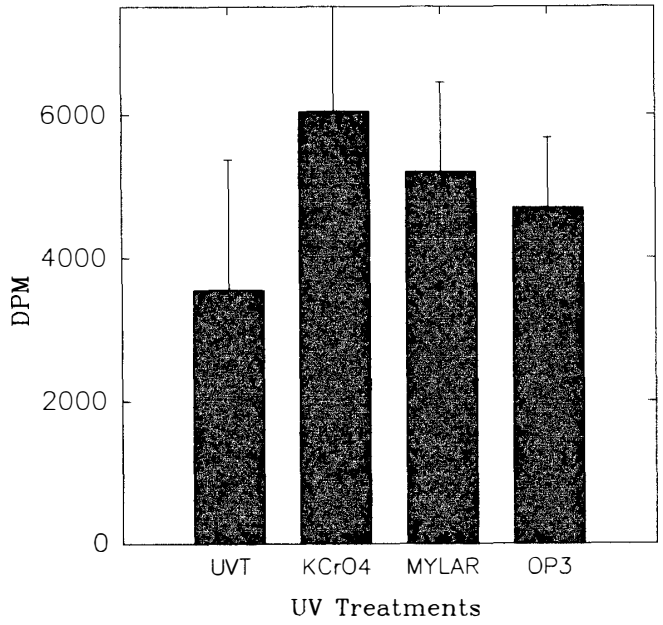

Fig. 8. ^{14}C (as sodium bicarbonate) uptake in mats exposed 6 days to different UV treatments. Legends as in Fig. 2.

Table 2. Photosynthetic characteristics of the mats after 11 days of UV treatment. Values are the mean of 2 replicates (standard error lower than 10%). α is the slope of the light limited portion of the Photosynthesis *vs.* Irradiance curve. P_{max} is the maximum value of oxygen production Compensation point is irradiance at which the net oxygen production (photosynthesis) equals the O_2 consumption (respiration).

Treatment	α (μmol O_2 cm^{-2} h^{-1})/ (μE m^{-2} s^{-1})	P_{max} (μmol O_2 cm^{-2} h^{-1})	Compensation point (μE m^{-2} s^{-1})
UVT	1.28	57 24	10
MYLAR	0.51	45.73	300
OP3	0.558	35.48	150
K	0.6	40.0	100

the net oxygen production (photosynthesis) equals the O_2 consumption (respiration). Mats under the full UV treatment (UVT) showed the minimum compensation point (10 μmol photon $m^{-2} s^{-1}$) and mats under just PAR and UVA (Mylar) had the maximum value (300 μmol photon $m^{-2} s^{-1}$).

Discussion

Laboratory experiments of UVB effects have typically been undertaken with artificial UV lamps that usually provide unnatural outputs that differ in quality and quantity from ambient sunlight. Therefore, the extrapolation of the information obtained under these circumstances to ecosystem level is not easy. We have carried out this study *in situ* to estimate the UVB effects on cyanobacterial mats under natural conditions. However, the use of the UV filters in the experiments only allowed to eliminate completely UVA and/or UVB and not to reduce partially the UVR. This fact may make difficult to extrapolate our results to an eventual UVR increase.

The concentrations of Chl *a* and Car determined in Casten Pond are in the range of that published previously on Antarctic cyanobacterial mats (VINCENT *et al.*, 1993a). However, the pigment increase detected in all the light treatments after 11 days of differential exposure may indicate growth of the photosynthetic community within the microbial assemblage or may be due to a chromatic adaptation in response to the shading produced by the sediment accumulated on the filters. Nevertheless, the stability of the ratio Car/Chl *a* between sampling dates suggests that during the experimental period there was no selective pigment adaptation.

The HPLC separation of lipophilic pigments showed a typical fingerprint (YACOBI *et al.*, 1996) for this kind of community, with very similar results to those described in VINCENT *et al.* (1993b). The lack of significant differences in the pigment fingerprint between treatments indicate that this cyanobacterial mat did not change, as a whole, their pigment composition. We did not analyze the pigment concentration along the core profile, and, as VINCENT *et al.* (1993a) have shown, the pigment distribution can change in depth.

The consistently lower concentration of PBP under UVT observed in our experiments is in agreement with the higher sensitivity of these pigments to UVB (QUESADA *et al*, 1995), although differences were not significant. LAO and GLAZER (1996) have demonstrated in laboratory experiments that photodestruction of phycobiliproteins is 4 orders of magnitude higher under 295 nm than under visible light.

The lack of significant differences between pigment concentrations in mats under UV treatments does not agree with the visual results. This discrepancy may be explained by considering a different allocation of the pigmented cells within the mat profile after the UV treatments. However, the core, as a whole, did not change in total concentration of pigments, although in the mat under OP3, pigmented cells might have migrated to the surface conferring a darker aspect. In order to validate this hypothesis more research has to be done looking at the position of pigments within the mat profile.

MAAs have been described as defenses against UV radiation. Our results indicate that the community studied was rich in the MAA porphyra-334. However, the concentration of porphyra-334 did not change significantly during our experimental

period in any of the treatments. This observation is consistent with longer-term (3 months) observations of Antarctic macroalgae which showed little change in MAA content over time (KARENTZ, unpublished). Similar observations have been made in marine invertebrates (SHICK *et al.*, 1991; GLEASON, 1993), suggesting that changes in MAA content do not occur in response to daily, weekly or monthly changes in light regime.

Physiological measurements of communities are good indicators of the biological state, because they can show metabolic adaptations that may affect dramatically ecological relationships. The measurements of photosynthesis (^{14}C uptake, and O_2 evolution) in this study had contradicting results. ^{14}C uptake data showed a decrease (non-significant) of photosynthesis under the full solar spectrum. Nevertheless, PI curves indicated that cells under these conditions had maximum photosynthetic capacity (P_{max}) and efficiency (α). This paradox might be resolved by considering that UVR maybe more effective at damaging the respiration processes (in both heterotrophic and autotrophic organisms) than photosynthesis. This hypothesis might be supported by the fact that the compensation point (irradiance at which net O_2 production is higher than the consumption) is at least one order of magnitude lower in mats exposed to the full solar spectrum than in those exposed to the other treatments, and this could be indicative of lower respiration rate in the former.

The low effects of UVR *in situ* shows that the extremely high sensitivity of many organisms to UVR in laboratory experiments (*e.g.* QUESADA *et al.*, 1995) is not necessarily a general feature in natural environments. The general lack of significant differences between treatments in our experiments could indicate a high innate tolerance to UV or an adaptation that has perhaps developed during the gradual increased irradiance associated with daily changes in daylength and solar zenith angle which are characteristics of the Antarctic during spring and summer. Moreover, our results could be a function of the short-term nature of the study.

In summary, our results indicated that there is little or no effect of partitioned ambient light regimes *in situ* on the cyanobacterial mat chosen for these experiments. We did not find any clear variation in the community structure, in the pigment characteristics, nor in the photosynthetic rates. We suggest that the respiration/photosynthesis ratio may be altered because of the high sensitivity of respiration to the UVR. Respiration is especially important in this ecosystem, as can be deduced from the low natural O_2 concentration recorded in Casten Pond at midday (lower than the saturation value). Stronger UVR increases could produce in this ecosystem an imbalance in the respiration/photosynthesis ratio which could lead to as yet unknown ecosystem effects.

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