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Photoreactivity of Dissolved Organic Matter from High-Mountain Lakes of Sierra Nevada, Spain*

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Abstract

The effect of many environmental stressors can be mediated by dissolved organic matter (DOM) properties. In this study, DOM from four high mountain lakes (two surrounded by meadows and two located on rocky terrain) was optically characterized and its photoreactivity was experimentally evaluated. To evaluate DOM photoreactivity, photobleaching rates of absorptivity, and fluorescence and their effects on DOM spectral properties were analyzed. Dissolved organic carbon (DOC) concentration ranged from 37 to 69 μM , absorptivity at 320 nm (a_{320}) from 0.60 to 3.09 m^{-1} , and fluorescence from 1.30 to 5.70 QSU. Photobleaching of absorptivity was significant only at 320 nm (a_{320}) resulting in half lives that varied from 2.6 to 6.7 d. Photobleaching of a_{320} was significantly higher for DOM from lakes located on rocky terrain than for DOM from lakes surrounded by meadows. Photobleaching of fluorescence emission at 450 nm (F_{450}) was significant only for three lakes and their half lives varied from 4.1 to 6.3 d. No significant differences were observed among the lakes studied. The changes over sunlight exposure of spectral slopes (S_{UV}), ratios of absorptivity at 250 nm to 365 nm ($a_{250}:a_{365}$) and ratios of fluorescence emission at 450 nm to 500 nm ($F_{450}:F_{500}$) did not show consistent trends with alternate increases and decreases. Lakes surrounded by meadows showed higher DOC concentrations, higher absorptivities, and lower a_{320} photobleaching coefficients, suggesting that these lakes could be less vulnerable to UVR than lakes located on rocky terrain.

Introduction

Multiple natural and anthropogenic stressors (acid rain, increased UVR, land-use change, global warming, etc.) affect lake biogeochemistry and biota (Gorham, 1996; Sommaruga-Wögrath et al., 1997; Breitburg et al., 1999). The impact of many of these stressors can be mediated by DOM (Yan et al., 1996; Schindler et al., 1996; Schindler and Curtis, 1997; Donahue et al., 1998; Williamson et al., 1999).

The nature of DOM influences the attenuation of sunlight in the water column and consequently determines photosynthetic potential and transmission of UVR (Morris et al., 1995; Morris and Hargreaves, 1997; Carpenter et al., 1998). The empirical models that relate UVR attenuation and DOC concentration (Scully and Lean, 1994; Morris et al., 1995) diverge significantly for low-DOC lakes. DOM optical properties (absorptivity and photoreactivity) and phytoplanktonic contributions have been suggested as plausible explanations of that divergence (Morris et al., 1995; Laurion et al., 1997; Morris and Hargreaves, 1997; Sommaruga and Psenner, 1997; Laurion et al., 2000).

Fulvic acids account for a major fraction of DOM in aquatic systems. The origin of this organic material determines its chromophoric and fluorophoric contents (McKnight et al., 1994, 2001). Fulvic acids derived from plant litter and soils generally contain a significant content of aromatic carbon (25–30% of total carbon) (Malcolm, 1990). In contrast, the aromaticity of micro-

bially-derived fulvic acids is lower (12–17%) (McKnight et al., 1994). Therefore, the relative contribution of allochthonous vs. autochthonous inputs to the total pool of DOM can influence its absorptivity and fluorescence.

The DOM absorption of sunlight can induce several reactions (photobleaching, photomineralization, photohumification, etc.). In general, DOM susceptibility to react with sunlight is termed photoreactivity. More specifically, photobleaching is the reduction of DOM capacity to absorb light or fluoresce which is caused by degradation of chromophoric or fluorophoric compounds, respectively. The higher the photobleaching rate, the greater the depth of UVR transmission in a lake (Morris and Hargreaves, 1997). The reverse reaction, sunlight-induced humification, has been also described in low DOC systems (Kieber et al., 1997; Benner and Biddanda, 1998). DOM photoreactivity has been related to intrinsic properties of DOM and water chemistry (Gao and Zepp, 1998; Reche et al., 1999; Bertilsson and Tranvik, 2000; Lindell et al., 2000). In summary, DOC concentration, absorption, and photoreactivity are major factors determining UVR transmission in the water column.

Alpine lakes are above treeline and typically have small catchment areas with poorly developed soils and sparse terrestrial vegetation. Therefore, DOC concentrations in these lakes are, usually, low and DOM is mostly derived from autochthonous sources (Baron et al., 1991; McKnight et al., 1997; Sommaruga et al., 1999; Laurion et al., 2000). However, allochthonous inputs can be notable during specific periods (e.g., snowmelt) or in lakes surrounded by meadows (Baron et al., 1991; Laurion et al., 2000). Information on photoreactivity of DOM from alpine lakes, to date, has not been reported. The alpine

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TABLE 1

Morphometric, chemical, and biotic characteristics of the lakes studied. PP is primary production and BP is bacterial production

Lakes	Altitude (m a.s.l.)	Surface (ha)	Catchment (ha)	Maximum depth (m)	pH	Conductivity ($\mu\text{S cm}^{-1}$)	k_d PAR (m^{-1})	Chlorophyll-a ^a ($\mu\text{g L}^{-1}$)	PP ^a ($\mu\text{gC L}^{-1}\text{h}^{-1}$)	BP ^a ($\mu\text{gC L}^{-1}\text{h}^{-1}$)
Aguas Verdes (AV)	3050	0.19	12.8	2.8	7.3	32.1	0.50	0.6 ^b	1.44	0.23
Río Seco (RS)	3020	0.42	9.9	2	8.7	25.9	0.41	0.17	4.28	0.11
Caldera (CA)	3050	2.10	23.5	7	8.5	34.7	0.41	0.34	3.53	0.08 ^c
Yeguas (YE)	2880	0.33	50	9.5	9.2	42.5	0.28	0.89	4.27	0.04

^a Data from Reche et al. (unpublished).

^b Datum from Morales-Baquero et al. (1999).

^c Datum from Reche et al. (1996).

landscape, besides providing low-DOC to lakes, is submitted to high incident UVR (Caldwell et al., 1980) suggesting that alpine lakes can be prone to photoreactions (Scully et al., 1997; Reche et al., 2000).

In this paper, optical properties of DOM from four high mountain lakes (two located on rocky terrain and two surrounded by meadows) were analyzed. DOM photoreactivity of each lake was determined measuring experimentally the photobleaching rates of absorptivity and fluorescence and the changes of its spectral properties. To evaluate the potential influence of autochthonous sources on the optical properties and the photoreactivities of lake DOM, identical characterizations and one experiment were performed using DOM from algal cultures. Finally, the sensitivity to UVR of the lakes surrounded by meadows as contrasted with the lakes located on rocky terrain was assessed.

Material and Methods

STUDY SITES

Four lakes of glacial origin from Sierra Nevada (Spain) ($36^{\circ}55' - 37^{\circ}15' \text{N}$, $2^{\circ}31' - 3^{\circ}40' \text{W}$) were selected for this study. Lakes are from 2880 to 3050 m a.s.l. on predominantly siliceous rocks and above treeline. Usually, they are ice covered from November to June. Aguas Verdes (AV) and Río Seco (RS) are partially surrounded by meadows (approx. 90 and 70% of lake perimeters, respectively). In contrast, Caldera (CA) and Yeguas (YE) are placed directly on rocky terrain. A higher contribution of DOM from allochthonous inputs is expected in lakes surrounded by meadows with respect to lakes located on rocky terrain.

Table 1 shows some morphometric, chemical, and biological characteristics of the lakes studied. More information can be also found in Morales-Baquero et al. (1999). Macrophytes and fish are absent in all four lakes.

SAMPLING AND ANALYTICAL METHODS

Each lake was sampled at a central station once during July of 1999. Underwater photosynthetically active radiation (PAR) was measured at 0.2-m depth intervals with a LiCor (LI 193SA) quantum sensor. Water samples were collected at the depth of 50% PAR attenuation and subsampled for DOC, absorptivity, fluorescence measurements, and to perform photobleaching experiments. Water for photobleaching experiments (2 L) was stored at approx. 4°C in the dark for 2 to 3 h until the laboratory was reached. Conductivity and pH were measured using a Crison conductance meter and pH meter.

Duplicate samples for DOC concentration were analyzed by filtering lake water through precombusted Whatman GF/F glass

fiber filters. The filtrate was collected in a combusted (>2 h at 500°C) flask, acidified with HCl (final pH < 2) and stored at 4°C in the dark until analysis. DOC concentrations of lake water samples were measured with a high-temperature catalytic oxidation method in a Shimadzu TOC analyzer (Model 5000) equipped with a Shimadzu platinumized-quartz catalyst for high sensitivity analysis (Benner and Strom, 1993). Samples were purged for 20 min to eliminate remains of dissolved inorganic carbon (DIC). Three to five injections were analyzed for each sample and blank (Milli-Q water). The blank value ($3.7 \mu\text{M}$) was subtracted of the average DOC value of the samples. Standardization of the instrument was done with potassium hydrogen phthalate (4-points calibration curve).

Duplicate samples for absorbance and fluorescence were filtered through Whatman GF/F filters. Absorbance scans from 250 to 700 nm were measured in 10-cm quartz cuvettes using a Perkin-Elmer Lambda 40 spectrophotometer connected to a computer equipped with UV-WINLAB software. Absorbances at specific wavelengths (250, 320, and 365 nm) were expressed as absorptivities (a_{250} , a_{320} , and a_{365}) in per meter (Miller, 1998). The ratios of absorptivities to DOC concentration (DOC-specific absorptivities) and of a_{250} to a_{365} ($a_{250}:a_{365}$) were calculated. DOC-specific absorptivity indicates the capacity of DOC to absorb sunlight. The ratio $a_{250}:a_{365}$ is considered as an index of relative size of DOM molecules (Strome and Miller, 1978; Morris and Hargreaves, 1997). High ratios indicate a high proportion of small molecules and low ratios a high proportion of large molecules.

The spectrum of each lake was plotted as \ln (absorptivity) vs. wavelengths, and the spectral slope for the ultraviolet waveband (S_{UV}) was determined from a standard linear regression of the data from 290 nm to 400 nm (Green and Blough, 1994). The slope is a measure of the rate at which absorptivity decreases at longer wavelengths (Miller, 1998). The higher the slope, the more accentuated is the decrease of the absorptivity at longer wavelengths.

Fluorescence emission spectra from 370 to 650 nm (excitation at 370 nm, slit width of 0.5 nm) were measured in a Perkin-Elmer LS50B spectrofluorometer using 1-cm quartz cuvette (rinsed twice with the sample). Fluorescence at 450 nm (F_{450}) was normalized to the Raman area (integral) to obtain fluorescence in Raman units (nm^{-1}) (Nieke et al., 1997). F_{450} was also expressed as quinine sulfate units (QSU), where $1 \text{ QSU} = 1 \mu\text{g L}^{-1}$ of quinine sulfate dissolved in 0.1 N H_2SO_4 . Five standards (1, 2, 5, 10, and $20 \mu\text{g L}^{-1}$) were used for the calibration curve. Milli-Q water was used as sample blank and 0.1 N H_2SO_4 as standards blank (Skoog et al., 1996). The ratio of the fluorescence at 450 nm with respect to 500 nm ($F_{450}:F_{500}$) and the wavelength of the emission maximum were also deter-

mined. $F_{450}:F_{500}$ can be considered as an index of fulvic acids origin (allochthonous vs. autochthonous). A ratio of ≈ 1.4 is typical for terrestrially derived fulvic acids, and a ratio of ≈ 1.9 is typical for microbially derived fulvic acids (derived from degradation of algae and bacteria). Microbially derived fulvic acids have fluorophores with a more sharply defined emission peak occurring at lower wavelengths than fluorophores of terrestrially derived fulvic acids (McKnight et al., 2001).

To assess the importance of the autochthonous signature on the optical properties of lake DOM, the same optical parameters were determined for DOM from continuous cultures of *Dictyosphaerium* sp. and *Cryptomonas* sp. These algae are not common in the lakes studied, but were selected because of the difficulty to isolate and grow *in situ* species. The values obtained could be considered as a reference for fresh autochthonous DOM. Both species were growing in a Z8 medium (Skulberg and Skulberg, 1990) at $20 \pm 2^\circ\text{C}$, with a photosynthetically active radiation (PAR) of $90 \mu\text{mol m}^{-2} \text{s}^{-1}$ and a 14:10 h LD cycle. A 130-ml sample from each culture was collected in a precombusted glass bottle and filtered through a $0.2 \mu\text{m}$ -Millipore filter at low pressure ($<15 \text{ cm Hg}$) to eliminate algae and bacteria. Aliquots for DOC concentration, absorbance, and fluorescence were prepared as for lake samples. DOC concentrations were measured in a Shimadzu TOC Analyzer (Model 5050) because of their high concentrations. Samples were acidified and purged for 3 min to eliminate DIC remains. Five injections were analyzed for each sample and blank (Milli-Q water). The blank value ($31 \mu\text{M}$) was subtracted.

EXPERIMENTAL DETERMINATION OF PHOTBLEACHING RATES

Lake waters were filtered through $0.2 \mu\text{m}$ -Millipore filters, immediately after we arrived to the laboratory, and stored at 4°C in the dark until next day when the experiments started. This filtration minimizes bacterial influence for at least 3 to 5 d (Skoog et al., 1996; Reche et al., 1999). A subtle contamination for absorptivity values (restricted to a narrow waveband around 275 nm) was caused by this filtration (Fig. 1). Absorptivity values of the experimental samples were corrected subtracting the absorptivity values of Milli-Q water filtered through $0.2 \mu\text{m}$ -Millipore filters.

Eighteen bottles for each lake (twelve 37-ml quartz and six 37-ml borosilicate bottles) were filled with the filtered water. Borosilicate bottles were black-tape covered for use as dark controls. All material was previously acid-washed and rinsed, at least twice, with Milli-Q water. Quartz bottles were spherical flasks with a mean pathlength (L) of 2.828 cm ($2 \sin 45^\circ$ radius).

To reduce differences in solar spectrum quality, which could modify photobleaching rates (Reche et al., 2000), all quartz bottles from all systems were incubated on a platform (on the laboratory roof) under natural sunlight (from sunrise to sunset) for 3 (AV, RS, and CA) or 4 (YE) sunny days. Dark bottles were located in a shady place. Two quartz- and one dark-bottles of each lake were sequentially removed at six time points during the exposure to obtain decay kinetics. Absorbance and fluorescence of each sequential sample were measured using methods described above. Since no significant changes in absorbance or fluorescence were detected in dark-bottles, we can attribute absorbance and fluorescence changes in quartz bottles to sunlight effect.

Incident sunlight energy ($\mu\text{E m}^{-2} \text{s}^{-1}$) was monitored with a portable spectroradiometer (LiCor Model LI-1800). Two mea-

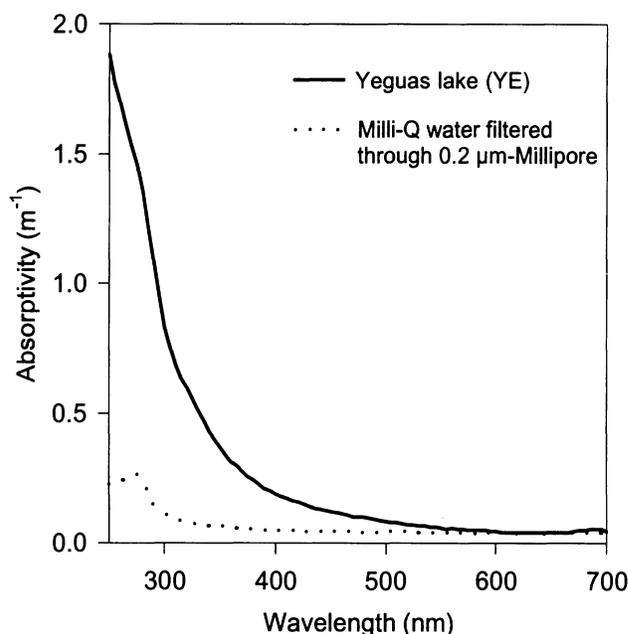


FIGURE 1. Absorptivities from 250 nm to 700 nm of Milli-Q water filtered through a $0.2 \mu\text{m}$ -Millipore filter using Milli-Q water as blank. Values are the average of three replicates. Absorptivities of DOM from the lake Yeguas (YE) have been included to scale the magnitude of the contamination.

surements were considered: total energy integrated from 300 to 700 nm and the energy at the specific wavelength of 320 nm.

DOM photoreactivity was evaluated determining the changes over sunlight exposure of absorptivity (a_{250} , a_{320} , and a_{365}), fluorescence (F_{450}), and spectral properties ($a_{250}:a_{365}$, S_{UV} and $F_{450}:F_{500}$) in the quartz bottles. Absorptivity changes usually fit negative exponential function (Reche et al., 1999). Therefore, absorptivity photobleaching coefficients (k_{ba}) are the slopes of the ln-linear regressions between absorptivities and cumulative incident or absorbed sunlight doses. These coefficients were calculated of three ways depending on the dose units: incident energy (E m^{-2} , 1st case), time (d, 2nd case) and energy absorbed at 320 nm (E m^{-3} , 3rd case). The general equation is:

$$a_{\lambda n} = a_{\lambda 0} e^{-k_{ba} D} \quad (1)$$

where $a_{\lambda 0}$ is initial absorptivity and $a_{\lambda n}$ is absorptivity (m^{-1}) at $\lambda = 250, 320$, or 365 nm after a cumulative sunlight dose D . D values were obtained by the addition of incident or absorbed sunlight energy over time exposure. K_{ba} values were expressed in time units (d^{-1}) converting incident sunlight doses in days:

$$k_{ba}(\text{d}^{-1}) = \frac{\ln \frac{a_{\lambda n}}{a_{\lambda 0}}}{t} \quad (2)$$

where t is $\text{E m}^{-2} \text{d}^{-1}$. From equation 2 absorptivity half life (hl_{λ}) (the time to reduce 50% of initial absorptivity) was calculated as:

$$hl_{\lambda} = \frac{\ln(0.5)}{k_{ba}(\text{d}^{-1})} \quad (3)$$

Fluorescence (F_{450}) photobleaching coefficients and half lives were calculated using the same equations.

Photobleaching rate coefficients for each lake can be influenced by the self-shading inside experimental bottles (Miller, 1998). Therefore, photobleaching coefficients of absorptivity at 320 were also calculated using the energy absorbed (Ea_{320}) inside

TABLE 2

Concentration of dissolved organic carbon (DOC) and absorptivity and fluorescence properties of DOM from the lakes studied (Aguas Verdes, Río Seco, Caldera, and Yeguas) and from two algal cultures (C_1 is *Dictyosphaerium sp.* and C_2 is *Cryptomonas sp.*)

	Aguas Verdes (AV)	Río Seco (RS)	Caldera (CA)	Yeguas (YE)	Algae (C_1)	Algae (C_2)
DOC (μM)	48	69	37	43	6983	5875
a_{250} (m^{-1})	6.52	5.04	2.74	1.89	28.49	16.92
a_{320} (m^{-1})	3.09	1.54	0.85	0.60	9.22	7.05
a_{365} (m^{-1})	1.57	0.78	0.39	0.30	5.03	3.53
$a_{250}:\text{DOC}$	0.136	0.073	0.074	0.046	0.004	0.003
$a_{320}:\text{DOC}$	0.064	0.022	0.023	0.014	0.001	0.001
$a_{365}:\text{DOC}$	0.033	0.011	0.011	0.007	0.001	0.001
$a_{250}:a_{365}$	4.15	6.46	7.02	6.30	5.66	4.79
$S_{\text{UV}} \times 10^{-3}$ (μm^{-1})	11.51	15.95	16.98	15.89	15.95	13.30
F_{450} (nm^{-1})	0.019	0.016	0.013	0.007	n.a.	2.047
F_{450} (QSU)	5.70	4.37	3.50	1.30	n.a.	23.14
$F_{450}:F_{500}$	1.46	1.73	1.85	4.05*	n.a.	n.c.
Emission peak (nm)	442	440	431	486*	n.a.	n.c.

* Values out of range for aquatic fulvic acids (McKnight et al., 2001).

n.a. not analyzed.

n.c. not comparable.

the experimental bottles. $E_{a_{320}}$ (E m^{-3}) was obtained using the equation proposed by Miller (1998):

$$E_{a_{320}} = E_{0\ 320}(1 - 10^{-a_{320}/2.303 L})S/V \quad (4)$$

where $E_{0\ 320}$ is incident sunlight dose at 320 nm (E m^{-2}), L (m^{-1}) is the mean pathlength of the experimental bottles (see above), S is surface area (m^2) of a columnated light beam passing through the sample, and V is the volume (m^3) of solution that was exposed to sunlight.

To assess how decisive can be the autochthonous contribution to determine DOM photoreactivity of the lakes, another photobleaching experiment was performed using DOM from an algae culture. The photobleaching coefficient obtained could be considered as a reference of photoreactivity of fresh autochthonous (phytoplanktonic) DOM. Water from a batch culture (stationary phase) of *Chlamydomonas kniepii* was filtered through 0.2 μm -Millipore filter to exclude algae and bacteria and was used to carry out one photobleaching experiment. *Chlamydomonas kniepii* was growing in BBM medium (Nichols and Bold, 1965) at $20 \pm 2^\circ\text{C}$ with a PAR of $134 \mu\text{mol m}^{-2} \text{s}^{-1}$ and a 14:10 h LD cycle. *Chlamydomonas kniepii* abundance in the culture was of 1.8×10^6 cell ml^{-1} . The days of sunlight exposure were not coincident with the days of the lake photobleaching experiments, although in both cases were sunny days of July. Photobleaching rate coefficients were calculated at the specific wavelengths of 250, 320, 365, and 530 nm using the same equations described above.

Results

OPTICAL CHARACTERIZATION OF DOM

DOC concentration ranged from 37 to 69 μM among the lakes studied. Absorptivities at the specific wavelengths considered are shown in Table 2. Lakes surrounded by meadows (AV and RS) showed higher DOC concentrations and absorptivities than lakes located on rocky terrain (CA and YE). DOC in the algal culture waters were two orders of magnitude (from 5875 to 6983 μM) higher than in lake waters. Absorptivities in the algal culture waters were from 3- to 10-fold higher than in lake

waters. The highest DOC-specific absorptivities were observed in AV and the lowest ones in YE. DOC-specific absorptivities for lakes were more than one order of magnitude higher than for the algal cultures (Table 2). The ratios of a_{250} to a_{365} and the S_{UV} values were similar for all lakes, except for AV that showed the lowest ratio and spectral slope (Table 2). The $a_{250}:a_{365}$ and S_{UV} values for the algal cultures were similar to the lake values (Table 2).

Fluorescence (F_{450}) varied from 0.007 nm^{-1} (1.3 QSU) in YE to 0.019 nm^{-1} (5.7 QSU) in AV. F_{450} values were higher in lakes surrounded by meadows than in lakes located on rocky terrain. The lowest $F_{450}:F_{500}$ ratio (typical values for DOM with significant allochthonous contribution) was observed for DOM from AV (Table 2). The wavelengths of the emission maximum varied from 431 nm in CA fluorescence spectrum to 442 nm in AV spectrum. The $F_{450}:F_{500}$ ratio for YE and the wavelength of its emission maximum were out of the typical range for aquatic fulvic acids (McKnight et al., 2001) indicating that other non-humic compounds probably are contributing to fluorescence.

DOM PHOTOREACTIVITY

Wavelength-specific photobleaching coefficients were calculated at 250, 320, and 365 nm. However, the coefficients were significant for all the lakes only at 320 nm. The variance of a_{320} losses explained by sunlight exposure was always below 75% (Table 3). Photobleaching coefficients at 320 ($k_{b\ 320}$) varied from -0.104 d^{-1} ($17.59 \times 10^{-4} [\text{E m}^{-2}]^{-1}$) in RS to -0.266 d^{-1} ($45.99 \times 10^{-4} [\text{E m}^{-2}]^{-1}$) in CA. These coefficients expressed as half lives of a_{320} ranged from 6.7 d to 2.6 d (Table 3). Photobleaching coefficients were statistically significant at 365 nm only for CA ($k_{b\ 365} = -0.251 \text{ d}^{-1}$, $P < 0.05$), and at 250 nm only for RS ($k_{b\ 250} = -0.062 \text{ d}^{-1}$, $P < 0.05$).

The coefficients obtained using the energy absorbed at 320 nm inside the experimental bottles (3rd case) varied almost one order of magnitude from 0.669 to 6.405 (E m^{-3}) $^{-1}$ (Table 3). Figure 2 shows the ln-linear regressions between a_{320} and energy absorbed at 320 nm for all lakes. The slopes ($k_{b\ 320}$ values) for DOM from the lakes surrounded by meadows (AV and RS) were conspicuously lower than the slopes for DOM from the lakes

TABLE 3

Slopes (photobleaching coefficients, $k_b \pm$ standard errors) of the ln-linear regressions between absorptivity at 320 nm (a_{320}) or fluorescence (F_{450}) and sunlight doses. The doses have been expressed as incident energy (1st case), time (2nd case) and, energy absorbed at 320 nm (3rd case)

Cases		Aguas Verdes	Río Seco	Caldera	Yeguas	<i>Ch. kniepii</i>	
a_{320}	1st	k_b ($E m^{-2}$) $^{-1} \times 10^{-4}$	25.98 ± 9.26	17.59 ± 4.69	45.99 ± 8.50	30.01 ± 8.98	n.d.
	2nd	k_b (d^{-1})	-0.148 ± 0.054	-0.104 ± 0.027	-0.266 ± 0.049	-0.175 ± 0.051	-0.058 ± 0.026
		hl^a	4.7 ± 1.7	6.7 ± 1.7	2.6 ± 0.5	4.0 ± 1.2	11.9 ± 5.2
		r^2	0.43	0.60	0.75	0.54	0.34
		P	<0.05*	<0.01**	<0.001***	<0.01**	<0.05*
	3rd	k_b ($E m^{-3}$) $^{-1}$	0.669 ± 0.227	0.788 ± 0.324	4.244 ± 0.894	6.405 ± 1.403	n.d.
r^2		0.47	0.37	0.69	0.68	n.d.	
P		<0.05*	<0.05*	<0.001***	<0.01**	n.d.	
F_{450}	1st	k_b ($E m^{-2}$) $^{-1} \times 10^{-4}$	30.7 ± 11.94	20.5 ± 5.37	19.40 ± 3.67	n.s.	n.d.
	2nd	k_b (d^{-1})	-0.169 ± 0.071	-0.120 ± 0.031	-0.110 ± 0.022	n.s.	n.d.
		hl	4.1 ± 1.7	5.8 ± 1.5	6.3 ± 1.3	n.s.	n.d.
		r^2	0.40	0.63	0.71	n.s.	n.d.
		P	<0.05*	<0.01**	<0.01**	n.s.	n.d.

^a hl is half live \pm standard error.

n.s. not significant.

n.d. not determined.

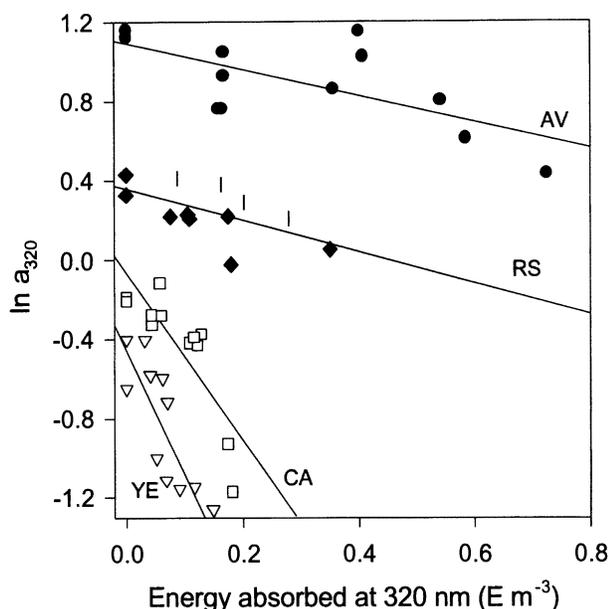
located on rocky terrain (CA and YE). To test if these slopes were statistically different among them, F -tests (Sokal and Rohlf, 1981) were performed (Table 4). $K_{b, 320}$ values were significantly higher (faster photobleaching) for DOM from CA or YE than from AV or RS. $K_{b, 320}$ values neither were significantly different between the lakes surrounded by meadows (AV vs. RS) nor between the lakes located on rocky terrain (CA vs. YE).

Wavelength-specific photobleaching coefficients were calculated at 250, 320, 365, and 530 nm for DOM from the *Ch.*

kniepii culture. The coefficient at 320 nm was also significant ($k_{b, 320} = -0.058$, $P < 0.05$) and lower (slower photobleaching) than for any lake DOM (Table 3). The coefficient at 365 nm was not significant ($P > 0.05$) and absorptivity at 250 nm and at 530 nm increased significantly ($P < 0.05$) over sunlight exposure with $k_{b, 250} = + 0.113 d^{-1}$ and $k_{b, 530} = + 0.168 d^{-1}$ (Fig. 3).

Lake waters for the experiments were filtered by 0.2 μm (removing algae and bacteria), consequently DOM spectral changes over sunlight exposure should be mostly related to photoreactions. Significant trends ($a_{250}:a_{365}$ ratio vs. exposure time or S_{UV} vs. exposure time) could not be established for any lake. However, the S_{UV} changes were smoother for DOM from lakes surrounded by meadows (Fig. 4A) than for DOM from lakes located on rocky terrain (Fig. 4B). The changes of the $a_{250}:a_{365}$ ratio for lake DOM were similar to S_{UV} changes. In the experiment with DOM from the *Ch. kniepii* culture, likewise lake DOM, the changes over sunlight exposure of $a_{250}:a_{365}$ ratio and S_{UV} did not show consistent trends.

Photobleaching of F_{450} and changes of $F_{450}:F_{500}$ ratio were also analyzed in the experiments. F_{450} kinetics also fit negative exponential functions in all experiments, except in YE. F_{450} coefficients (slopes of ln-linear regressions) ranged from $-0.110 d^{-1}$ ($19.40 \cdot 10^{-4} [E m^{-2}]^{-1}$) in CA to $-0.169 d^{-1}$ ($30.7 \cdot 10^{-4}$



- AGUAS VERDES (AV) □ CALDERA (CA)
- ◆ RIO SECO (RS) ▽ YEGUAS (YE)

FIGURE 2. Regression lines between ln absorptivity at 320 nm (a_{320}) and the energy absorbed at 320 nm. Filled symbols correspond to the lakes surrounded by meadows and open symbols to the lakes located on rocky terrain. The slopes of these regression lines are the $k_{b, 320}$ values that are shown in Table 3 (3rd case).

TABLE 4

Results of the F -tests performed to determine whether the photobleaching coefficients of absorptivity at 320 nm were significantly different among the lakes. F_s is the experimental value that was compared with the theoretical value for 1 and 20 degrees of freedom

	AV	RS	CA	YE
AV		$F_s = 0.015$	$F_s = 5.471$	$F_s = 10.887$
		$P = 0.905$ n.s.	$P < 0.05^*$	$P < 0.01^{**}$
RS			$F_s = 23.597$	$F_s = 21.847$
			$P < 0.001^{***}$	$P < 0.001^{***}$
CA				$F_s = 2.949$
				$P = 0.101$ n.s.

n.s. not significant.

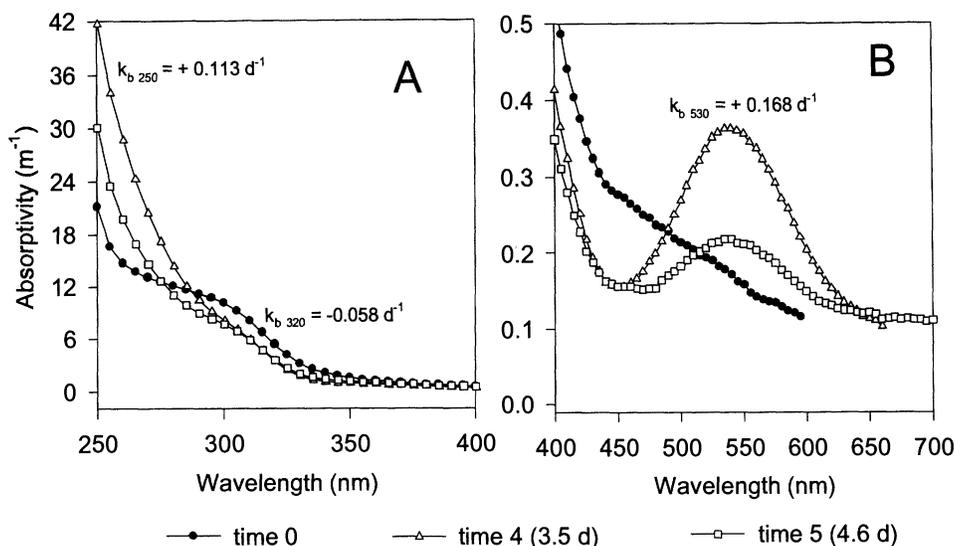


FIGURE 3. Absorptivity changes over wavelengths in the ultraviolet (A) and in the visible (B) wavebands in the photobleaching experiment with DOM from a *Chlamydomonas kniepii* culture. To simplify only three times (t_0 , t_4 , and t_5) of the sunlight exposure are plotted, although all data (t_0 , t_1 , t_2 , t_3 , t_4 , and t_5) have been included in the regression analysis to obtain the photobleaching or probably photohumification coefficients. These coefficients at 250, 320, and 530 nm ($k_{b\ 250}$, $k_{b\ 320}$, and $k_{b\ 530}$) and their standard errors are shown.

[E m⁻²]⁻¹) in AV (Table 3). In contrast to a_{320} photobleaching, F_{450} photobleaching was higher for DOM from lakes surrounded by meadows (AV and RS) than for CA. However, no significant differences among the coefficients were found. Those coefficients expressed as half lives of F_{450} ranged from 6.3 d to 4.1 d (Table 3). The changes over sunlight exposure of the $F_{450}:F_{500}$ ratio did not present a clear trend with alternate increases and decreases. The wavelengths of the emission maximum ranged from 425 to 442 nm for AV; from 440 to 457 nm for RS; from 431 to 432 nm for CA and were out of range at any time of exposure for YE.

Discussion

LAKE DOM PROPERTIES

Aquatic ecosystems sensitivity to UVR is a function of several factors including: incident UVR, underwater UVR trans-

mission, lake morphometry and mixing regime which determine water volume affected, etc. (Madronich et al., 1995; Morris et al., 1995; Scully et al., 1997; Reche et al., 2000; Whitehead et al., 2000). In particular, underwater UVR transmission is determined by concentration, absorptivity and resistance to photodegradation of DOM molecules (Scully and Lean, 1994; Morris et al., 1995; Morris and Hargreaves, 1997; Reche et al., 1999).

DOC concentrations and absorptivities, as it was expected, were higher in the lakes surrounded by meadows than in the lakes located on rocky terrain. These values were as low as the values reported for other alpine lakes (Baron et al., 1991; McKnight et al., 1997; Sommaruga et al., 1999; Laurion et al., 2000). However, DOC-specific absorptivities in the lakes studied were slightly higher than in other alpine lakes (Morris et al., 1995; Zagarese et al., 1999; Laurion et al., 2000) and were close to values observed in some forest lakes (Morris et al., 1995;

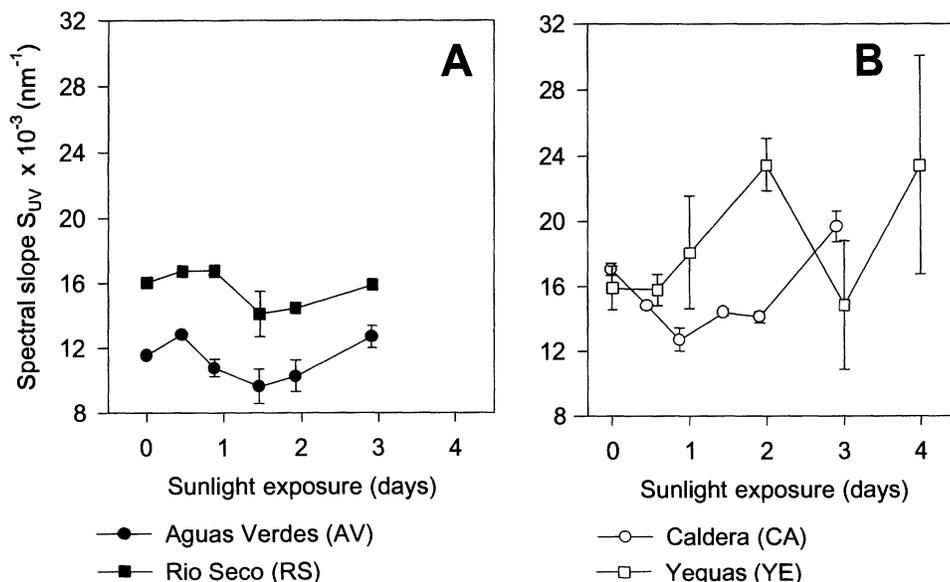


FIGURE 4. Changes over sunlight exposure of the spectral slope (S_{UV}) of DOM from the lakes surrounded by meadows (A) and from the lakes located on rocky terrain (B). Bars represent standard errors.

Reche et al., 1999). Unexpectedly, DOC-specific absorptivities did not show pronounced differences between lakes surrounded by meadows and lakes located on rocky terrain.

DOC-specific absorptivities in the algal cultures (fresh DOM) were considerably lower (more than one order of magnitude) than for any lake. This fact suggests that in-lake processes should lead to an increase over time of DOC-specific absorptivities, particularly in lakes located on rocky terrain. These last lakes only receive terrestrial inputs during ice melt. Some processes can be proposed to elucidate why DOC-specific absorptivities in the lakes surrounded by meadows (more terrestrial DOC) were similar to the values obtained for the lakes located on rocky terrain (more microbially derived DOC) and were in the same range that forest lakes. Bacteria seem to consume preferentially DOM with low aromaticity (Sun et al., 1997). Therefore, aromatic DOM will probably accumulate throughout ice-free period. On the other hand, the high incident UVR in the alpine landscape could also promote high rates of photohumification from smaller precursors derived from algal DOM (Hedges, 1988) or through oxidation, condensation, and transformation of existing biopolymers (e.g., polyunsaturated lipids from plankton) (Kieber et al., 1997). It has been observed that enhanced UVB can induce phytoplankton production of fatty acids (Wängberg et al., 1999). These compounds can easily induce humification (Kieber et al., 1997). The significant increases of absorptivities at 250 nm and 530 nm during the photobleaching experiment using DOM from *Ch. kniepii* culture (Fig. 3) suggest that sunlight could transform fresh algal DOM increasing its absorptivities. Another and non exclusive alternative is that phytoplankton, in these lakes submitted to high UVR, releases a proportionally higher quantity of absorbing compounds (e.g., mycosporine-like). It is, now, evident that phytoplankton can significantly influence on UVR attenuation in alpine lakes (Sommaruga and Psenner 1997; Laurion et al., 2000). These two last processes could be more pronounced in lakes where DOM is mostly of autochthonous (phytoplanktonic) origin (i.e. lakes located on rocky terrain).

DOM PHOTOREACTIVITY

DOM photoreactivity was based on the absorptivity and fluorescence photobleaching coefficients and the sunlight-induced changes of spectral properties ($a_{250}:a_{365}$ ratio, S_{UV} , and $F_{450}:F_{500}$ ratio). The first difference between photoreactivity of DOM from the alpine lakes studied and other systems was the heterogeneous response across wavelengths of the absorption spectrum and the low variance of absorptivity losses explained by sunlight doses (<75%). DOM from forest lakes, usually, photoreacts decreasing absorptivities at any wavelengths of the spectrum (Morris and Hargreaves, 1997; Reche et al., 2000) and the variance values are higher (>90%). However, in this study, photobleaching coefficients at the selected wavelengths were significant for all the lakes only at 320 nm. The absence of significant results at other wavelengths could be related to the existence of sunlight-induced humification that could counteract the photobleaching effects on absorptivities.

The balance between photobleaching and sunlight-induced humification could also explain the absence of a clear trend over sunlight exposure of the $a_{250}:a_{365}$ ratios, S_{UV} values, or $F_{450}:F_{500}$ ratios. It is not evident if photobleaching induces an increase (Vodacek et al., 1997; Whitehead et al., 2000) or a decrease (Morris and Hargreaves, 1997; Gao and Zepp, 1998) of spectral slopes. The different range of wavelengths selected to calculate spectral slopes and the inclusion or exclusion of biota has con-

tributed to this ambiguity (Markager and Vincent, 2000). A growing number of works have documented that these two processes occur in natural waters (Morris and Hargreaves, 1997; Vodacek et al., 1997; Benner and Biddanda, 1998).

DOM from lakes located on rocky terrain (CA and YE) showed higher $k_{b,320}$ values and the changes of $a_{250}:a_{365}$ ratio and S_{UV} were more accentuated than DOM from lakes surrounded by meadows (RS and AV). To explain this higher photoreactivity of DOM from lakes located on rocky terrain, several hypothesis can be argued: (1) they have stronger autochthonous (DOM enriched in compounds with low specific absorptivity) influence that will induce a higher photoreactivity; (2) they have higher mean depths and/or (3) they have different water chemistry. The first option seems not to be very plausible. The differences in DOC-specific absorptivities between both type of lakes were not as pronounced as to explain one order of magnitude variability in photobleaching coefficients. Moreover, photobleaching of DOM from the *Ch. kniepii* culture was noticeably lower than photobleaching of any lake DOM. Then, fresh autochthonous DOM could comparatively have low photoreactivity, although this photoreactivity could be different for other algae species or nutritive conditions. Lakes located on rocky terrain have higher mean depths than lakes surrounded by meadows. Lake morphometry and mixing regime can significantly affect the volume of water susceptible to photoreact (Reche et al., 2000; Whitehead et al., 2000). DOM from AV or RS (shallower lakes) has been probably exposed to sunlight more time and could be more photorefractory than DOM from CA or YE (deeper lakes). In addition, the slightly higher ionic strength of the lakes located on rocky terrain could also lead to higher photobleaching rates. Several works have reported that the ionic environment where the DOM is dissolved can influence its photoreactivity (Gao and Zepp, 1998; Reche et al., 1999; Bertilsson and Tranvik, 2000). On the other hand, seasonal effects derived from the duration and onset of the ice-free period for each lake could also have influenced the DOM sunlight exposure and, then, its photoreactivity. This seasonal influence was tried to be minimal by sampling all lakes at the same day.

The photobleaching rates of fluorescence emission at 450 nm (F_{450}) were similar to the values obtained in other systems (Skoog et al., 1996). Unexpectedly, F_{450} photobleaching coefficients were higher for DOM from lakes surrounded by meadows, but were not significantly different among the lakes studied. These results contrast with those ones obtained for a_{320} photobleaching. Absorptivity and fluorescence are distinctive DOM properties. DOM molecules are able to absorb at different wavelengths (usually decreasing exponentially as wavelengths increase), whereas only a fraction of DOM are able to fluoresce. Components of higher molecular weight absorb strongly at 250 nm but fluoresce weakly, while humic fractions of lower molecular weight fluoresce intensely per unit absorbance (Stewart and Wetzel, 1980, 1981). Therefore, the divergence between a_{320} and F_{450} photobleaching results could be related to variable molecular weights of the DOM from each lake. Moreover, fluorescence coefficients only can be calculated using incident sunlight doses instead of energy absorbed inside the experimental bottles. Then, fluorescence coefficients could be different values depending on the energy absorbed in each case.

Lakes surrounded by meadows showed higher DOC concentrations, higher absorptivities and lower a_{320} photobleaching coefficients (DOM was more resistant to photodegradation per photon absorbed). These results suggest a lower sensitivity to UVR of the lakes surrounded by meadows with respect to the lakes located on rocky terrain. Nevertheless, more extensive (in-

creasing lake diversity) and seasonal studies are required to outline more accurately patterns of lake-sensitivity to UVR. Moreover, other factors (besides optical properties of DOM) as lake morphometry, mixing regime or watersheds influence should be also integrated to obtain those general patterns.

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