

NOTE

Photoreactivity and bacterioplankton availability of aliphatic versus aromatic amino acids and a protein

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ABSTRACT: In batch culture experiments with natural bacterial assemblages collected from a humic-rich lake (Lake Neusiedl, Austria), labile organic nitrogen containing model substrates (alanine [Ala], an aliphatic amino acid, tryptophan [Trp], an aromatic amino acid, and bovine serum albumin [BSA], as protein) were added to 0.2 µm filtered lake water prior to exposure (for 9 h) to surface levels of the full range of solar radiation or being held in the dark. These organic nitrogen species were chosen to investigate compound-specific differences in the photochemical transformation of labile dissolved organic matter (DOM) and its subsequent availability to bacteria. 'Photocoloring' or humification in the Trp-amended water exposed to natural solar radiation and significant dissolved organic carbon (DOC) loss (120 µM C over 9 h exposure) resulted, after inoculation of the natural bacterial assemblage, in a lower maximum bacterial abundance in the previously solar radiation-exposed treatments as compared to the dark control. In contrast, the absorbance characteristics of solar-irradiated Ala- and BSA-amended water were almost identical to the unamended control and to the Ala- and BSA-amended treatments kept in the dark. Also, no significant difference in the maximum bacterial abundance of the solar radiation-exposed Ala- and BSA-amended treatments was detectable as compared to the corresponding dark controls. Our data indicate that Trp is a potential source of solar radiation-mediated humification in Lake Neusiedl.

KEY WORDS: Shallow lake · Dissolved organic matter · UV radiation · Photoreactivity · Bioreactivity

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In the surface layers of aquatic systems, ultraviolet (UV) radiation acts on planktonic organisms as well as on dissolved organic matter (DOM) (Herndl et al. 1997). Generally, UV radiation in inland and coastal waters is attenuated more rapidly than in open marine systems because of the higher dissolved and particulate organic matter content of the former. The 10 %

radiation level of the UV-A radiation range (320 to 400 nm) is at around 50 m in the open subtropical ocean (Obernosterer et al. 1999). In many estuarine waters and freshwater systems, the 10 % level for UV-A radiation is frequently less than 2 m (Kirk 1994). In the humic-rich Lake Neusiedl (Austria), for example, the 10 % UV-B (280 to 320 nm) and UV-A level of surface radiation is at 8 and 30 cm depths, respectively (Reitner et al. 1997).

In surface waters, bacteria and phytoplankton are more affected by UV radiation than other organisms due to their small size. While a number of phytoplankton species have UV-absorbing pigments, such as scytonemin and mycosporine-like amino acids (Garcia-Pichel 1994, Karentz et al. 1994), bacteria have no such UV-protective pigments. However, Aas et al. (1996) and Sommaruga et al. (1997) found that in the presence of phytoplankton, the inhibition of bacterial incorporation of leucine and thymidine is less pronounced during exposure to UV radiation than in the absence of phytoplankton. This has been attributed to a combined effect of shading by phytoplankton and the release of DOM by phytoplankton.

UV radiation affects bacterioplankton not only directly but also indirectly via the photochemical alteration of DOM. Photolytic cleavage of DOM leads to the formation of low molecular weight DOM and inorganic compounds, which can be efficiently utilized by bacterioplankton. Utilizable low molecular weight compounds produced from parent DOM upon exposure to solar radiation are free amino acids (Amador et al. 1989), carbonyl compounds (Moran & Zepp 1997, Bertilsson & Tranvik 1998, Obernosterer et al. 1999), ammonium (Bushaw et al. 1996) and phosphate (Francko & Heath 1982). Moreover, exposure of DOM to solar radiation might also result in the complete photo-oxidation of dissolved organic carbon (DOC) to

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carbon dioxide (Miller & Zepp 1995, Granéli et al. 1996) and carbon monoxide (Mopper et al. 1991, Valentine & Zepp 1993). Reactive oxygen species, such as hydrogen peroxide (H_2O_2) and hydroxyl radicals (OH) (Zafiriou et al. 1984, Cooper & Lean 1992, Zika et al. 1993), are also formed and act as photosensitizers on DOM and impair the functioning of the membranes of microorganisms.

Recent studies have demonstrated that the exposure of labile DOM to UV radiation renders it more refractory (Keil & Kirchman 1994, Naganuma et al. 1996, Tranvik & Kokalj 1998, Obernosterer et al. 1999, Pausz & Herndl 1999), suggesting that photochemical reactions are also involved in the production of biorefractory DOM (Kieber et al. 1997). As shown by Keil & Kirchman (1994) and Tranvik & Kokalj (1998), the presence of natural DOM is essential to convert labile DOM (proteins and algal exudates) into refractory DOM upon exposure to solar radiation. The balance between the solar radiation-induced formation of bioavailable substrates and the formation of biorefractory compounds occurring at the same time ultimately determines the net effect of the photochemically altered DOM on bacterioplankton utilization (Herndl et al. 1997).

The photoreactivity of individual compounds is determined by their absorption characteristics. Thus, we assumed that major differences in the photoreactivity of selected organic nitrogen compounds exist. The aim of the present study was, therefore, to follow the photochemical alteration of specific, originally labile organic nitrogen compounds and its influence on their bioreactivity.

MATERIALS AND METHODS

Sampling location. A detailed description of the limnology of Lake Neusiedl is given in Löffler (1979). Briefly, Lake Neusiedl (47°42'N, 16°46'E) is the largest shallow, alkaline, brown-water lake in central Europe (115 m above sea level [a.s.l.], surface area 321 km², maximum depth 1.8 m, mean depth 1.17 m, pH 8.5 to 9.1). About 52% of the lake is covered by the reed *Phragmites australis*; within this reed belt there are numerous reedless ponds of variable size. The water level of the lake is controlled by precipitation (500 to 700 mm yr⁻¹) and evaporation (Boroviczény et al. 1992). Frequent wind-induced resuspension of the sediment results in a high concentration of suspended solids in the water column during the ice-free period (Secchi depth ≈ 0.2 m). During winter when the lake is ice covered for up to 3 mo, the concentration of the suspended solids declines due to reduced water column turbulence. Reedless ponds within the reed belt, such

as the Ruster Poschn (surface area 40 000 m²), are generally more sheltered from wind. Consequently, resuspension of the sediments is lower, resulting in higher transparency of the water column (Secchi depth ≈ 0.6 m) than in the open lake. Due to the shallow water column of Lake Neusiedl, the water temperature can change rapidly in spring and fall.

Sampling. Water samples were taken at 0.5 m depth in the Ruster Poschn with cleaned (1 N HCl, rinsed 3 times with water from the sampling site prior to collecting the sample) 10 l polycarbonate flasks in the summer of 1999 and 2000. Concurrently with the sampling of the water, water temperature at the sampling site was measured. The water samples were brought back to the laboratory in an insulated box in the dark and processed within 30 min.

Influence of solar radiation on the bioavailability of dissolved free amino acids and a model protein to bacterioplankton. Lake water (6.5 l) was gently filtered first through a combusted (450°C for 4.5 h) Whatman GF/F glass fiber filter (100 mm filter diameter) and then through a pre-rinsed 0.2 µm polycarbonate filter (Millipore, 90 mm filter diameter). All the glassware used was thoroughly acid washed (in 1 N HCl), rinsed with double-distilled water and combusted (450°C for 4.5 h). The filtrate was subsequently dispensed into four 2 l glass flasks (1.5 l of the filtrate in each flask). Three of these flasks were amended with 500 µM C (final conc.) of one of the model substrates. In terms of carbon, the concentration of the added substrates was about one-third of the original DOC concentration of the lake water. L-alanine (Ala; 89 Da; Sigma, lot 57H0124) as a representative of an aliphatic amino acid and L-tryptophan (Trp; 204 Da; Sigma, lot 48H0576) as an aromatic amino acid were used as model substrates for free amino acids, while bovine serum albumin (BSA, Sigma, A 0281) served as a model protein. One treatment was left unamended and served as a control. Ten milliliter subsamples were taken from each treatment (Ala-, Trp- and BSA-amended water and the unamended control) for DOC analysis (described below). Then, the water of each flask was split and half of the volume was transferred into quartz tubes (750 ml capacity, 3.4 cm inner diameter, stoppered at both ends with sterile Teflon stoppers) and exposed to surface levels of natural solar radiation. The remaining half of the water was incubated in quartz tubes wrapped in aluminum foil to serve as a dark control. All tubes were incubated horizontally in the floating tray with about a 1 cm water layer above the upper end of the tubes for 9 h from 07:00 to 16:00 h on cloudless days. Thereafter, subsamples from the different treatments were taken for DOC and to determine the absorbance characteristics of the DOM. Subsequently, 720 ml of the solar radia-

tion-exposed water and the corresponding dark control of each treatment was transferred into Erlenmeyer flasks and inoculated with 80 ml of 0.8 μm filtered (Millipore, polycarbonate, 47 mm filter diameter) water from the sampling site to compare the bioavailability of the model substrates after exposure to solar radiation to that of the corresponding dark controls. These batch cultures were kept in the dark at *in situ* temperature and subsampled for bacterial abundance at 6 to 8 h intervals for a total period of 68 to 80 h. At the end of these incubations, subsamples were taken again for DOC and to determine the absorbance characteristics of the DOM. In total, 8 experiments were performed in the summers of 1999 and 2000.

Additionally, Trp (500 μM C final conc.) was added to Milli-Q water and incubated as described above, and the absorbance characteristics were compared with the corresponding Trp-amended lake water to determine the role of photosensitizers potentially present in the lake DOM.

Enumeration of bacteria. Ten milliliter subsamples were fixed with 3% (vol/vol, final conc.) concentrated formalin. Depending on the bacterial abundance, 1 to 3 ml was used to enumerate bacterial abundance by 4',6-diamidino-2-phenylindole (DAPI) staining (Porter & Feig 1980) and epifluorescence microscopy at 1250 \times magnification. Bacteria were enumerated on duplicate subsamples. At least 600 bacteria were enumerated per filter.

Determination of DOC. Immediately after filtering the samples for DOC analysis through combusted Whatman GF/F filters, the 10 ml samples were acidified with 50 μl of 1 N HCl and stored frozen. Prior to analysis, the acidified samples were thawed and the DOC concentration was determined using a Shimadzu TOC-5000 after sparging the samples with CO_2 -free air for 5 min. Standards were prepared with potassium hydrogen phthalate (Kanto Chemical Co. Inc., Kyoto, Japan). A platinum catalyst on quartz was used (Benner & Strom 1993). All DOC analyses were performed at least in triplicate.

Absorbance characteristics of DOC. Before and after exposure of the water samples to the different radiation regimens, the absorbance characteristics of the DOM were measured. Absorption spectra were measured against distilled water from 250 to 500 nm using a Beckman 640-I and a 5 cm light path (Lindell et al. 1995). Also, the absorption ratio of 250:365 nm was calculated to determine possible differences and shifts in the molecular size spectrum of the different treatments (Steward & Wetzel 1981).

RESULTS

Absorbance characteristics of solar radiation-exposed DOM amended with model molecules

The absorbance characteristics of Ala- and BSA-amended 0.2 μm filtered water (Fig. 1B,D) were almost identical to those of the unamended lake DOM (Fig. 1A) with no major changes detectable upon exposure to the full range of solar radiation for 9 h as compared to their corresponding dark controls (Fig. 1A,B,D). Trp-amended water held in the dark showed a pronounced slope in absorbance between 400 and 290 nm (Fig. 1C). However, exposure of Trp-amended water to natural solar radiation provoked a further increase in absorbance in the wavelength range between 450 and 300 nm (Fig. 1C) as compared to the Trp-amended water held in the dark. This change in the optical properties upon exposure to solar radiation was even visible by naked eye as the color of the Trp-amended water turned to light brown after exposure. This drastic change in the absorbance characteristics of Trp upon exposure to solar radiation was caused by an interaction of the added Trp with indigenous DOM, as

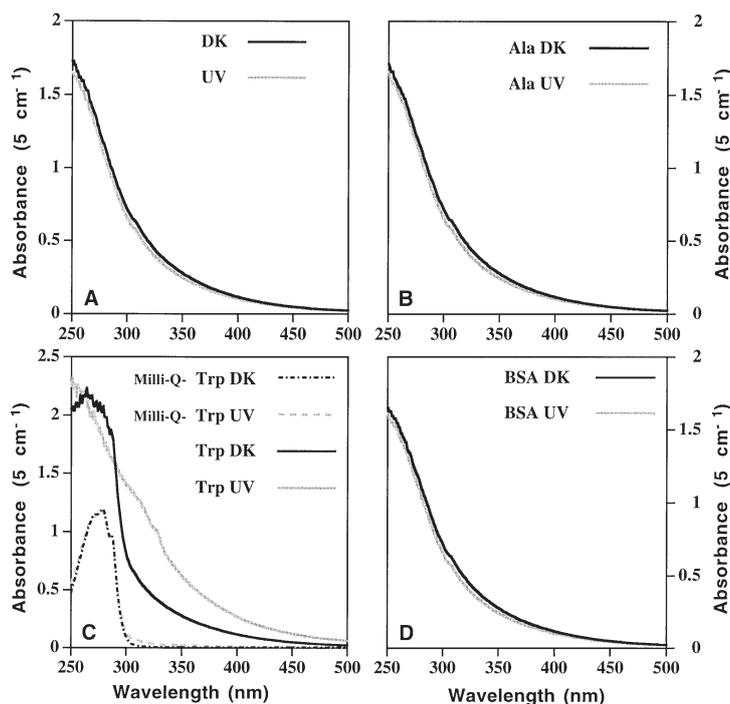


Fig. 1. Typical example (from 2 June 2000) of the absorbance characteristics of (A) indigenous dissolved organic matter (DOM) and the (B) alanine (Ala)-amended, (C) tryptophan (Trp)-amended and (D) bovine serum albumin (BSA)-amended water held in the dark (DK, black lines) or exposed to the full range of surface level solar radiation (UV, gray lines) over a diurnal cycle (for 9 h). The absorption of Trp-amended Milli-Q water is shown by dotted lines (C)

no differences in the absorbance characteristics of Trp dissolved in Milli-Q water were detectable between solar radiation-exposed and dark treatments (Fig. 1C).

The 250:365 nm absorbance ratios were highest in the Trp treatment (Table 1) prior to the exposure (mean \pm SD: 9.51 ± 0.81) and not significantly different from those obtained for the dark Trp treatment (9.35 ± 0.70 , Wilcoxon matched pair, $p = 0.1834$, $n = 8$). Both absorbance ratios of these Trp treatments were significantly higher than those of the unamended (7.72 ± 0.56), the Ala- (7.62 ± 0.51) and the BSA-amended dark treatments (7.46 ± 0.69 , Wilcoxon matched pair, $p = 0.0117$, $n = 8$) (Table 1). The 250:365 nm absorbance ratios of the solar radiation-exposed Trp-amended lake water (ranging from 4.23 to 5.78) were significantly lower than those of the dark Trp treatment, which ranged from 8.41 to 10.19 (Wilcoxon

matched pair, $p < 0.05$). Solar exposure of the unamended and Ala- and BSA-amended water to solar radiation, however, always led to significantly higher ratios than in the corresponding dark treatments (Wilcoxon matched pair, $p < 0.05$) (Table 1).

DOC decline in lake water amended with model molecules upon solar radiation

Exposure of 0.2 μm filtered lake water either unamended or amended with Ala, Trp or BSA to surface levels of natural solar radiation for 9 h resulted in a significant decline in DOC only in the radiation-exposed Trp-amended treatment. Mean DOC concentration declined from 1.93 ± 0.10 mM ($n = 8$) to 1.81 ± 0.09 mM DOC ($n = 8$), i.e., by about $13.3 \mu\text{M DOC h}^{-1}$.

Table 1. Summary of the absorbance ratios (250:365 nm) measured before (T_0) and after (T_1) exposure of the different treatments (unamended [UA] and alanine [Ala]-, tryptophan [Trp]- or bovine serum albumin [BSA]-amended 0.2 μm filtered lake water) to full solar radiation (UV) or incubated in the dark (DK)

Date (mo/d/yr)	UA T_0	UA DK T_1	UA UV T_1	Ala T_0	Ala DK T_1	Ala UV T_1	Trp T_0	Trp DK T_1	Trp UV T_1	BSA T_0	BSA DK T_1	BSA UV T_1
06/24/99	6.60	6.99	7.62	6.70	6.99	7.58	8.09	8.41	5.78	6.65	6.10	7.55
07/03/99	7.53	7.51	8.16	7.49	7.46	8.16	9.20	9.18	5.21	7.48	7.41	8.11
05/11/00	7.42	7.01	7.47	7.37	6.92	7.38	9.26	8.48	4.23	7.30	6.85	7.37
05/17/00	7.36	7.39	7.90	7.25	7.27	7.86	8.92	8.88	5.34	7.26	7.22	7.81
06/02/00	7.60	7.71	8.39	7.58	7.71	8.35	9.26	9.31	5.41	7.60	7.64	8.32
06/08/00	8.29	8.23	8.97	8.20	8.20	8.97	10.27	10.19	5.75	8.22	8.17	8.94
06/14/00	8.54	8.50	8.89	8.49	8.09	8.81	10.55	10.16	5.53	8.70	8.07	8.84
06/20/00	8.41	8.39	9.20	8.41	8.33	9.23	10.51	10.19	5.45	8.45	8.25	9.14
Mean	7.72	7.72	8.33	7.69	7.62	8.29	9.51	9.35	5.34	7.71	7.46	8.26
SD	0.61	0.56	0.61	0.59	0.51	0.63	0.81	0.70	0.46	0.65	0.69	0.62
Minimum	6.60	6.99	7.47	6.70	6.92	7.38	8.09	8.41	4.23	6.65	6.10	7.37
Maximum	8.54	8.50	9.20	8.49	8.33	9.23	10.55	10.19	5.78	8.70	8.25	9.14

Table 2. Summary of bacterial batch culture experiments. The maximum bacterial abundance of each experiment is given in $N \times 10^5 \text{ ml}^{-1}$ for the different treatments (UA and Ala-, Trp- or BSA-amended) exposed to the full spectrum of solar radiation (UV) or incubated at *in situ* temperature in the dark (DK). The maximum bacterial abundance of the water previously exposed to solar radiation is also given as a percentage of the corresponding dark treatment. ND: not determined due to growth of flagellates

Date (mo/d/yr)	UA DK	UA UV	% of DK	Ala DK	Ala UV	% of Ala DK	Trp DK	Trp UV	% of Trp DK	BSA DK	BSA UV	% of BSA DK
06/24/99	14.3	22.1	154.4	45.2	46.8	103.4	67.3	18.1	26.9	53.2	93.1	175.1
07/03/99	12.3	13.2	107.4	49.6	43.7	88.1	72.2	23.8	33.0	70.0	ND	ND
05/11/00	25.7	42.4	165.3	50.6	44.5	87.9	61.9	22.1	35.7	46.5	39.6	85.1
05/17/00	21.7	24.1	111.2	42.2	59.8	141.6	45.2	36.2	80.1	78.2	54.6	69.8
06/02/00	18.4	20.6	111.7	46.1	44.7	97.0	31.3	13.9	41.8	59.4	53.4	90.0
06/08/00	11.6	18.8	162.4	34.2	27.1	79.2	49.2	19.3	39.3	64.7	47.9	73.9
06/14/00	13.3	28.9	217.0	42.7	42.4	99.2	47.7	18.6	38.9	55.2	ND	ND
06/20/00	10.5	9.0	85.9	39.8	31.7	79.7	57.4	17.4	30.4	80.4	56.4	70.2
Mean	16.0	22.4	139.4	43.8	42.6	97.0	54.0	21.1	40.8	63.5	57.5	94.0
SD	5.4	10.2	42.9	5.3	9.9	20.1	13.3	6.9	16.6	12.1	18.5	40.6
Minimum	10.5	9.0	85.9	34.2	27.1	79.2	31.3	13.1	26.9	46.5	39.6	69.8
Maximum	25.7	42.4	217.0	50.6	59.8	141.6	72.2	36.2	80.1	80.4	93.1	175.1

Changes in the bioavailability of Ala, Trp and BSA upon exposure to solar radiation

Inoculation of indigenous bacterioplankton to unamended lake water previously exposed to solar radiation (for 9 h) led to a significantly higher maximum bacterial abundance than in the corresponding dark control (139% of the dark; Wilcoxon matched pair, $p = 0.0251$, $n = 8$) while no significant differences in bacterial abundance between radiation-exposed Ala- or BSA-amended lake water and the corresponding dark controls were detectable (Wilcoxon matched pair, $p_{\text{Ala}} = 0.3270$, $p_{\text{BSA}} = 0.3454$) (Table 2, Fig. 2). However, in the previously solar radiation-exposed Trp-amended treatment, maximum bacterial abundance ($21.1 \pm 6.9 \times 10^5 \text{ ml}^{-1}$) was significantly lower than in the Trp-amended dark control ($54.0 \pm 13.3 \times 10^5 \text{ ml}^{-1}$) (Wilcoxon matched pair, $p = 0.0117$, $n = 8$) reaching, on average, only 41% of the maximum bacterial abundance of the corresponding dark control (Table 2).

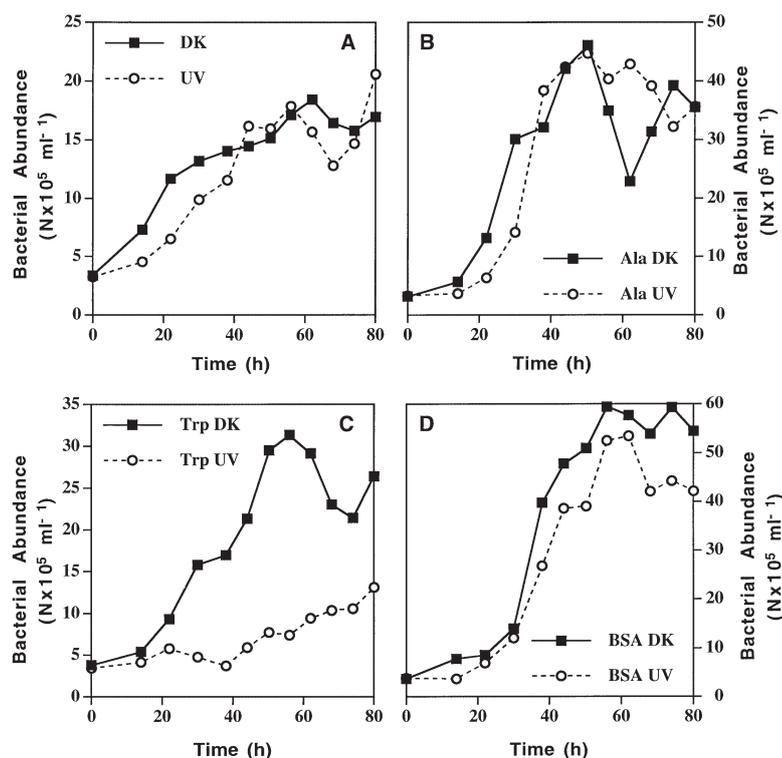


Fig. 2. Example of the development of bacterial abundance in a batch culture (from 2 June 2000) with (A) unamended, indigenous DOM and culture amended with (B) Ala, (C) Trp or (D) BSA and exposed for a full diurnal cycle to surface levels of solar radiation prior to inoculating the natural bacterial assemblages. Open symbols indicate bacterial abundance in the treatments exposed to full solar radiation prior to inoculating the bacterial community (UV); full symbols represent the bacterial abundance in the treatments held in the dark (DK) prior to inoculation

DISCUSSION

Influence of solar radiation on substrate availability for bacterioplankton

On the one hand, UV radiation can stimulate bacterial growth by cleaving readily utilizable low molecular weight compounds from the parent DOM (Lindell et al. 1995, Wetzel et al. 1995, Obernosterer & Herndl 2000). On the other hand, DOM might also be rendered more biorefractory (Keil & Kirchman 1994, Naganuma et al. 1996, Kieber et al. 1997, Pausz & Herndl 1999, Obernosterer & Herndl 2000). Tranvik & Kokalj (1998) showed that fresh algal extracts became less available to the microbial community after UV radiation in the presence of humic substances. Besides the presence of indigenous DOM, the chemical structure of the labile DOM could also have a major influence on the photochemical transformation and its subsequent availability to bacteria. Our model substrates used in this study (Ala, an aliphatic amino acid, Trp, an aromatic amino acid, and BSA, a protein) were chosen to mimic the structural diversity of dissolved organic nitrogen compounds present in the natural environment.

The 'photocoloring' or humification of the Trp-amended water exposed to natural solar radiation is indicated by the increase in absorption in the lower photosynthetically active radiation (PAR) and throughout the UV range (Fig. 1C). This drastic change is caused by interactions between the aromatic amino acid and the indigenous DOM, as no differences in the absorbance characteristics of Trp in Milli-Q water were detectable. In contrast, the absorbance characteristics of the solar radiation-exposed Ala- and BSA-amended water were almost identical to those of the unamended control and of the treatments kept in the dark (Fig. 1). The significantly lower 250:365 nm absorbance ratio of the irradiated Trp treatment also indicates an increase of the high molecular weight compounds (Table 1). Exposure of Trp-amended 0.2 μm filtered lake water also resulted in a significant DOC loss (120 μM C) over the 9 h incubation period, indicating again that photoreactivity of the Trp-amended treatment resulted in the humification and a reduced carrying capacity of bacteria as compared to the dark control (Table 2, Fig. 2). Concurrently, part of the organic carbon is directly oxidized into inorganic

carbon. The loss of 120 μM C during the exposure to surface levels of solar radiation is similar to the oxidation rate found for humic-rich lake water by Granéli et al. (1996, 1998).

The exposure of the unamended and Ala- and BSA-amended water to natural solar radiation led to significantly higher absorbance ratios (250:365 nm) than in the corresponding dark treatments (Table 1). This reflects most likely a shift in molecular weight distribution toward smaller molecules (Strome & Miller 1978, DeHaan 1993). Several studies have shown that these low molecular weight substances formed by photo-degradation of DOM can be used efficiently by natural bacterial communities (Lindell et al. 1995, Moran & Zepp 1997, Reitner et al. 1997). In our batch culture experiments, however, a significant increase in maximum bacterial abundance was only found in the unamended treatment exposed to solar radiation as compared to the dark control. In the Ala- and BSA-amended treatments no increase in the carrying capacity for bacteria was detectable (Table 2). Apparently, solar radiation led to the release of easily utilizable compounds from the indigenous DOM while UV radiation had no further stimulatory effect on Ala- and BSA-amended treatments. In general, irrespective of the exposure to solar radiation, Ala and BSA amendments resulted, on average, in a 3 to 4 times higher maximum bacterial abundance (Table 2).

The question now is whether the model amino acids we used in the experiments are of significance for the system investigated. Bacterioplankton in Lake Neusiedl mainly obtain their substrate from non-phytoplankton sources (Reitner et al. 1999). It has been estimated that phytoplankton contribute at most 20% to the substrate requirements of bacterioplankton in Lake Neusiedl and that the vast majority of bacterial substrate is derived from DOM produced by the reed and its periphytes (Reitner et al. 1999).

The Shikimate pathway in plants is an important production pathway for aromatic molecules (as phenylalanine, tyrosine and Trp) (Richter 1996). The primary production of the reed *Phragmites australis* amounts to 1.3 to 8.2 g C m^{-2} reed d^{-1} (Kvet & Husak 1978), and about 55% of Lake Neusiedl is covered by *P. australis* (Löffler 1979). Thus, the average reed primary production for the entire lake is in the range of 0.7 to 4.5 $\text{g C m}^{-2} \text{d}^{-1}$. As only up to 10% of the reed production is harvested, the majority of the reed production enters the lake. In *P. australis*, Ala concentration amounts to 3 mg g^{-1} dry weight (DW) (9 to 48 $\text{mg m}^{-2} \text{d}^{-1}$), the aromatic phenylalanine amounts to 2.5 mg g^{-1} DW (7.5 to 40 $\text{mg m}^{-2} \text{d}^{-1}$) and the aromatic tyrosine amounts 1.6 mg g^{-1} DW (4.8 to 25.6 $\text{mg m}^{-2} \text{d}^{-1}$) (Kvet & Westlake 1998). If only 0.1% of the Ala reaches the water column through the leaching processes of *P. aus-*

tralis, then the daily Ala input into the water amounts to approximately 5 to 27 nM d^{-1} , which is in the range of measured Ala and Trp concentrations (~ 10 nM) in the water of Lake Neusiedl (author's unpubl. data). Assuming steady state concentrations of these amino acids, this means that their pool is turned over roughly once a day. Thus, we concluded that these 2 amino acid species are of ecological significance for the lake system and that, therefore, Trp might be a significant source of solar radiation-mediated humification in Lake Neusiedl.

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