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## Benthic photosynthesis in an acidic mining lake (pH 2.6)

**Abstract**—Natural neutralization of acidic mining lakes is usually limited by the availability of organic carbon. We investigated whether benthic photosynthesis could contribute to primary production in an acidic mining lake (pH 2.6). The occurrence and light dependence of benthic photosynthesis in the lake was investigated using oxygen microelectrodes. Oxygen microprofiles measured in light and darkness were significantly different, indicating photosynthetic activity. The photic zone was 300  $\mu\text{m}$  thick and the highest photosynthetic activity was found at the sediment surface, which was covered by a dense layer of diatoms. These algae, predominantly *Eunotia* spp. and *Pinnularia obscura*, were found to be adapted to low light intensities. The community compensation irradiance was  $6.8 \mu\text{E m}^{-2} \text{s}^{-1}$ , corresponding to an annual mean compensation depth of 1.8 m. These results imply that 13% of the lake area could have a net efflux of oxygen from the sediment. Even at an irradiance as low as  $1.2 \mu\text{E m}^{-2} \text{s}^{-1}$ , photosynthetic activity was detected. The relatively low light requirements for benthic photosynthesis in this acidic environment may be due to an efficient absorption of red light, the dominant wavelength available in this ferric iron-rich lake. Our results suggest that benthic photosynthesis can play an important role in the biogeochemistry of acidic mining lakes.

In mining areas, the oxidation of pyrite and marcasite associated with coal or metal ores leads to the formation of acid mine drainage (AMD). Lakes fed by AMD, either by groundwater or surface flow, are usually extremely acidic with a pH ranging from 2 to 4. In these lakes the pH is buffered by ferric iron:  $\text{Fe}^{3+} + 3\text{H}_2\text{O} \rightleftharpoons \text{Fe}(\text{OH})_3 + 3\text{H}^+$ , and the high iron content of the water leads to the typical reddish color of such lakes. An understanding of the ecosystem structure and function of these lakes is essential for the development of appropriate remediation strategies (Geller et al. 1998).

Enclosure experiments and in-situ observations indicate that the process of natural neutralization within acidic lakes depends on the amount of organic carbon available as a substrate for iron and sulfate reduction and on lake mixing and oxygen supply (Davison et al. 1995; Klapper and Schultze 1995). Therefore, primary production could influence the acidity of these lakes by producing organic carbon and liberating oxygen. Planktonic primary production in acidic mining lakes is usually low ( $2.7 \text{ mmol C m}^{-2} \text{ d}^{-1}$ , Gyure et al. 1987;  $0.08\text{--}16.5 \text{ mmol C m}^{-2} \text{ d}^{-1}$ , Lessmann et al. 1999)

because of low phytoplankton biomass and low biomass-specific production in these lakes (Nixdorf and Kapfer 1998; Lessmann et al. 1999). However, existing estimates of primary production only take into account pelagic photosynthesis. It is not known if, and to what extent, photosynthesis by benthic algae contributes to the primary production of acidic mining lakes. In a literature survey, about half of the lakes reviewed had benthic algal production equal to or higher than phytoplankton production (Vadeboncoeur et al. 2001). Mining lakes are typically shallow. In such lakes, benthic photosynthesis can make a significant contribution to carbon fixation (Sand-Jensen and Borum 1991). The present study was undertaken to determine whether, and to what extent, benthic photosynthesis takes place in an acidic mining lake.

The study was carried out in Mining Lake 111 (ML111) in the Lusatian mining district in Germany ( $51^{\circ}29'\text{N}$ ,  $13^{\circ}38'\text{E}$ ). The lake has a surface area of  $0.11 \text{ km}^2$ , a mean depth of 4.7 m, and a maximum depth of 10.2 m (Büttner et al. 1998). The lake pH was 2.6 and the titratable acid ( $\text{K}_{\text{BS}2}$ ) was 15.5 mM. Concentrations of  $\text{SO}_4^{2-}$ ,  $\text{Fe}^{3+}$ , and  $\text{Al}^{3+}$  were considered high at 12.5 mM, 2.5 mM, and 1.5 mM, respectively (Friese et al. 1998; Herzsprung et al. 1998). Acidity is supplied continuously by groundwater inflow. No natural neutralization of the water has been observed since the formation of the lake in 1958.

On 8 August 2000, two sediment cores were collected at a water depth of 7 m and transported at  $4^{\circ}\text{C}$  to a climate chamber. Four hours after sampling, the cores were immersed in an aquarium containing original lake water at an in situ temperature of  $9^{\circ}\text{C}$ . The water in the aquarium was continuously bubbled with air containing 5%  $\text{CO}_2$ . Concentration of  $\text{CO}_2$  increased from 4.8 to  $10.3 \text{ mg C L}^{-1}$  over the course of the experiments.  $\text{CO}_2$  was not assumed to limit photosynthesis and fell within the range of in situ concentrations at the depth sampled ( $6.1\text{--}16.6 \text{ mg C L}^{-1}$ ). The cores were preincubated for 12 h at a photosynthetically available radiation (PAR) of  $1.7 \mu\text{E m}^{-2} \text{ s}^{-1}$ , corresponding to typical in situ PAR measured 7 m deep on a cloudy summer day (assuming subsurface PAR  $700 \mu\text{E m}^{-2} \text{ s}^{-1}$ ). A specially designed optical device, consisting of halogen and fluorescent lamps, colored acetate transparencies, and a layer of circulating deionized water, was used to simulate the characteristic red light spectrum (Fig. 1a). PAR was measured

using intercalibrated spherical quantum sensors in the lab (QSL 101, Biospherical) and on several occasions in the lake (SPQA, Li-Cor). Additionally, the solar radiation was measured continuously over the course of 2000 by a meteobuoy (Aanderaa 2770). We converted the solar radiation to subsurface PAR by applying an empirical factor derived from field measurements where  $1 \text{ W m}^{-2}$  solar radiation corresponds to  $1.84 \mu\text{E m}^{-2} \text{ s}^{-1}$ . The spectral light distribution in the lake and in the incubator was measured using a UW1800

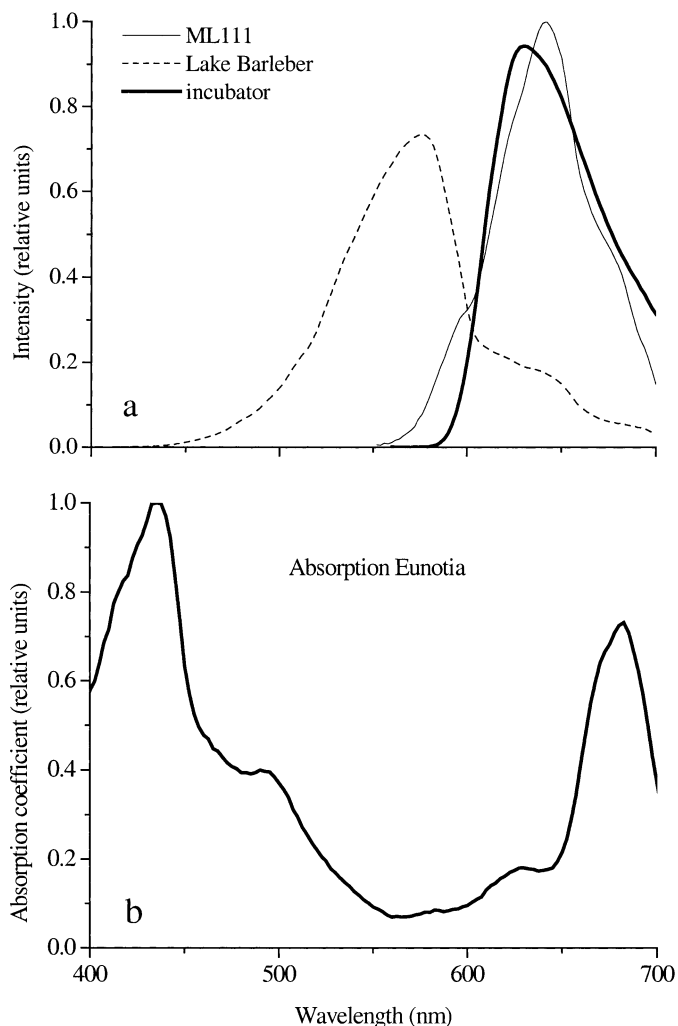


Fig. 1. (a) The spectral light distribution in Mining Lake 111 (7 m depth, 17 October 2000) and in the incubator used for this study. For comparison, a green light-dominated spectrum of a non-acidic mesotrophic gravel pit lake is shown (Lake Barleber, 7 m depth, 11 May 2001). The lake spectra were measured on cloudless days at midday. The lower panel (b) shows the wavelength dependence of the light absorption coefficient of a single *Eunotia exigua* cell taken from one of the sediment cores. All spectra were standardized to the same PAR—area below lines in (a) assumed to be equal—or maximum absorption coefficient (b). We estimated the rate of light absorption ( $J$ ) for each wavelength interval ( $J_\lambda = I_\lambda A_\lambda$ , where  $I_\lambda$  is PAR and  $A_\lambda$  is the absorption coefficient, 5-nm interval). Integrated over the wavelength spectrum, the algae in ML111 absorbed 1.53 times more photons than algae with a similar absorption characteristic in Lake Barleber.

Table 1. Oxygen flux and photosynthesis for two sediment cores from Mining Lake 111 in light ( $15.4$  and  $15.8 \mu\text{E m}^{-2} \text{ s}^{-1}$  for core 1 and 2, respectively) and in dark. Positive values indicate fluxes from sediment into water.

	Rate ( $\text{mmol m}^{-2} \text{ d}^{-1}$ )	
	Core 1	Core 2
Oxygen flux in dark	$-11.7 \pm 1.6$	$-5.8 \pm 0$
Oxygen flux in light	12.9	24.2
Community net photosynthesis	24.8	35.16
Community gross photosynthesis	47.5	84.3

spectrophotometer (Li-Cor). The pigment content of the sediment was determined by high-performance liquid chromatography (HPLC). To obtain the absorption spectra of the algae, a microscope photometer (MPM 400, Zeiss) was employed. Oxygen was measured with commercially available Clark-type microelectrodes (MASCOT, Bremen, Germany) with tip diameters of  $20 \mu\text{m}$ .

The sediment surface was covered by a dense layer of diatoms. These diatoms were primarily *Eunotia exigua* and *Pinnularia obscura*, but *E. steineckeii* and *E. tenella* were also identified. The chlorophyll *a* (Chl *a*) content of the sediment was  $52 \text{ mg m}^{-2}$  in core 1 and  $72 \text{ mg m}^{-2}$  in core 2. In order to determine whether there was an effect of light on the oxygen distribution in the sediment, we illuminated cores 1 and 2 with irradiances of  $15.4$  and  $15.8 \mu\text{E m}^{-2} \text{ s}^{-1}$ , respectively. Oxygen microprofiles measured in the light were different from those measured in the dark (Fig. 2). With light, an oxygen oversaturation at the sediment–water boundary was observed, as is typical for benthic photosynthesis (Revsbech and Jørgensen 1986). Benthic oxygen production resulted in a net flux of oxygen from the sediment into the water (Table 1). Fluxes were calculated from the oxygen gradient in the diffusive boundary layer using a diffusion coefficient of  $1.53 \times 10^{-5} \text{ cm}^2 \text{ s}^{-1}$  (Broecker and Peng 1974). Community net photosynthesis was determined as the flux of oxygen out of the photic zone (Wenzhöfer et al. 2000) using a measured sediment porosity of 0.9. Gross benthic photosynthesis was measured with oxygen microelectrodes using the light–dark shift method (Revsbech et al. 1981). The volume-specific rates were converted to an area-specific rate by summing up the gross rates measured in  $100\text{-}\mu\text{m}$ -thick sediment layers. Gross community photosynthesis, measured by the light–dark shift technique, was compared with net community photosynthesis. The results indicated that in cores 1 and 2, 48 and 59%, respectively, of the oxygen produced was respired in the photic zone. The difference between gross rate and net rate is rather low compared to other habitats and is indicative of the low respiratory activity in the mining lake sediment (Table 2). The sediment photic zone was  $300 \mu\text{m}$  thick, and the highest activity was observed at the sediment surface (Fig. 2). By applying the procedure of Berg et al. (1998) to our dark profiles, we found that oxygen consumption was also highest at the sediment surface. Approximately 50% of the oxygen consumption activity in the sediment was located in the photic zone. Both measured oxygen fluxes and photosynthetic rates were at the lower end of a range of literature values cited for various

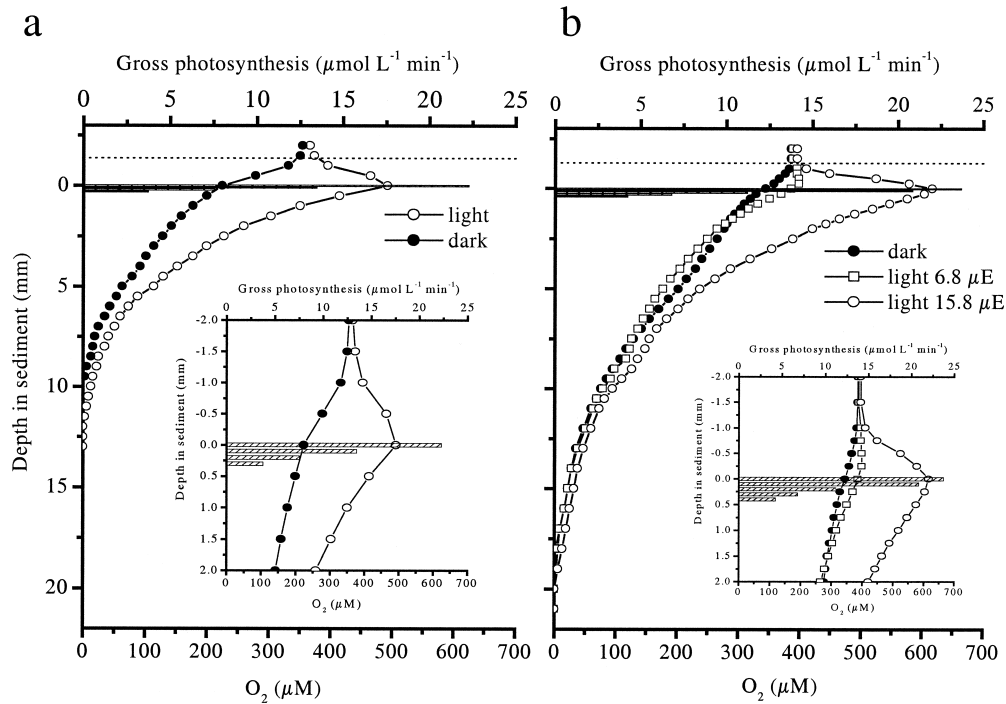


Fig. 2. Vertical profiles of oxygen in the sediment under light and dark conditions and the vertical distribution of gross photosynthesis (columns) measured in two different sediment cores (a, b). Irradiance was 15.4 (a, core 1) and 15.8  $\mu\text{E m}^{-2} \text{s}^{-1}$  (b, core 2). In core 2, oxygen was also measured at an irradiance of 6.8  $\mu\text{E m}^{-2} \text{s}^{-1}$ . The dotted line marks the benthic boundary layer. The insert shows a magnification of the sediment–water boundary. No gross photosynthesis could be detected below 0.3 mm (core 1) and 0.4 mm (core 2).

habitats (Tables 2, 3). Similar fluxes are reported for Lake Fuchskuhle, which is an acidic lake with a pH of 4.6 (Kühl et al. 1998). The low level of biological activity resulted in a deep penetration of oxygen into the sediment (Fig. 2). After the addition of mercury chloride to the overlying water, light had no effect on the oxygen profile observed, indicating that all of the activity was biotic. Our measurements suggest that benthic diatoms were able to carry out photosynthesis despite the acidic conditions prevailing in ML111. However, the irradiance of 15.8  $\mu\text{E m}^{-2} \text{s}^{-1}$  we employed was high compared with in situ PAR at the sampled depth.

At an irradiance of 6.8  $\mu\text{E m}^{-2} \text{s}^{-1}$ , which approximates the maximum potential PAR at the sampling depth, we found no measurable gradient of oxygen in the benthic boundary

layer (Fig. 2b). These results suggest that there was no net oxygen flux between the sediment and water. Under these conditions oxygen production equals oxygen consumption in the sediment. Thus, the compensation irradiance of the photosynthetic benthic community was assumed to be 6.8  $\mu\text{E m}^{-2} \text{s}^{-1}$ . From a review of several studies, the mean value for photosynthetic light compensation of phytoplankton was determined to be 6.7  $\mu\text{E m}^{-2} \text{s}^{-1}$  (Sand-Jensen and Borum 1991). When solar radiation and PAR attenuation ( $I_d = I_0 0.8785 e^{-0.8397d}$ ,  $r^2 = 0.99$ ;  $I_d$  and  $I_0$  are PAR at depth ( $d$ ) and below the surface, respectively) were combined, this compensation irradiance was calculated to correspond to a depth of 1.8 m in the annual mean irradiance profile for ML111. During the year, the compensation depth varied be-

Table 2. Biofilm photosynthesis in different habitats.

Habitat	Net rate (mmol $\text{m}^{-2} \text{d}^{-1}$ )	Gross rate (mmol $\text{m}^{-2} \text{d}^{-1}$ )	Reference
Marine sediment		192	Revsbech et al. 1981
Marine sediment	42		Wenzhöfer et al. 2000
Wadden Sea sediment		168–648	Revsbech et al. 1988
Hot spring		840	Revsbech and Ward 1984
Diatom biofilm	26	260	Jensen and Revsbech 1989
Tidal sediment	59	202	Epping et al. 1998
Epilithic biofilm	120–210	324	Glud et al. 1992
ML111	30	66	This study

Table 3. Oxygen fluxes at the sediment–water boundary in different habitats. Negative values signify oxygen uptake by the sediment.

Habitat	O <sub>2</sub> flux (mmol m <sup>-2</sup> d <sup>-1</sup> )	Reference
Intertidal estuary	–84 to –449	Baillie 1986
Skive Fjord (Denmark)	–11	Berg et al. 1998
Lake Vilhelmsborg (Denmark)	–42	Jensen et al. 1994
Lake Fuchskuhle (Germany)	–12	Kühl et al. 1998
Biofilm treatment plant	–94	Kühl and Jørgensen 1992
Mining Lake 111	–9	This study

tween 0.7 m in January and 3.0 m in June. Furthermore, when the area–depth relationship for ML111 was applied (Büttner et al. 1998), it was estimated that 13% of the lake's surface area could support an oxygen-producing benthic community. It was assumed that temperature stratification did not affect photosynthesis under light-limiting conditions (Steemann Nielsen and Jørgensen 1968). Gross photosynthesis was linearly related to irradiance (Fig. 3). We were able to measure gross photosynthesis down to a light intensity of 1.2  $\mu\text{E m}^{-2} \text{s}^{-1}$ . During summer (May–July), this irradiance occurred at 7 m for 8–9 h d<sup>-1</sup>.

Iron-rich waters generate an unusual spectral profile. The absorption spectrum of *Eunotia exigua*, however, was not different from spectra typical for diatoms growing in non-acidic lakes (Fig. 1). Despite the narrow light spectrum in ML111, there was a better spectral overlap between ambient light and algal absorption than observed in a nonacidic lake. For a given PAR, the algae in ML111 could use 1.53 times more photons than in the nonacidic lake. This light absorption efficiency may compensate for a reduced photosynthetic quantum efficiency. The latter was assumed to be a consequence of enhanced metabolic losses under acidic conditions (Turner et al. 1991).

In August 1999, we compared the transparency of five acidic mining lakes in the Lusatian area. Transparencies

ranged from 0.67 to 0.41 m<sup>-1</sup>, with ML111 having the lowest transparency. Thus, benthic photosynthesis might prove to be even more important in other mining lakes.

Benthic oxygen production has important implications for sediment diagenesis and the biogeochemistry of acidic lakes. Microbial oxidation of ferrous iron at the sediment–water boundary is a major source of protons and, thus, enhances lake acidification. In ML111, a diffusive flux of ferrous iron of 0.8 mmol Fe<sup>2+</sup> m<sup>-2</sup> d<sup>-1</sup> from the deeper sediment layers into the oxic surface sediment was measured (Koschorreck unpubl. data). Benthic photosynthesis can produce enough oxygen to stimulate or translocate microbial iron oxidation in the sediment. Further investigations should determine how and under which conditions benthic photosynthesis influences iron oxidation in the sediment (Epping et al. 1998). Studies are also needed to investigate whether alternating oxic and anoxic conditions in the sediment create a diurnal, internal redox cycle of iron, with reduction (alkalinity production) taking place at night and oxidation (acidity production) occurring during the day.

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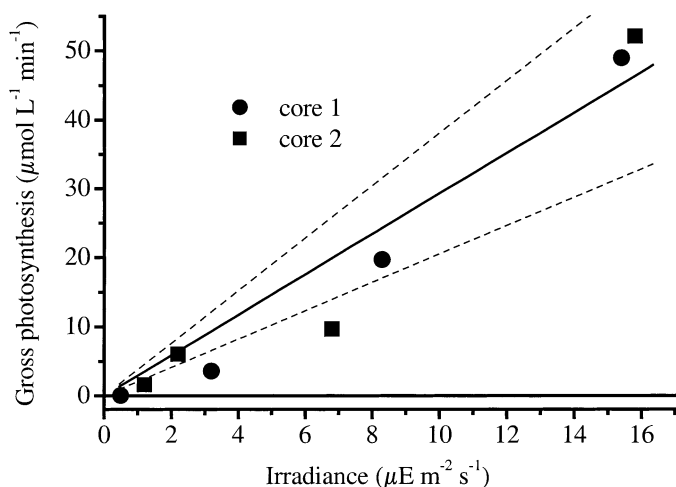


Fig. 3. The dependence of benthic community gross photosynthesis on irradiance. The dotted lines show the 95% confidence limits for data from both cores.

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