Photosynthetic activity of epilithic algal communities in sections of the Torna stream (Hungary) with natural and modified riparian shading

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Abstract The photosynthetic activity of epilithon grown in the Torna-stream (Hungary) was studied. Samples were collected from natural sections with closed canopy and natural stream bed and from modified sections with trapezoid river bed and shores lacking riparian vegetation. We assumed that human modifications would have a significant impact on epilithic photosynthesis, and therefore expected to observe corresponding changes in photosynthesis–irradiance (P–I) parametric. The laboratory P–I measurements were carried out monthly between April 2008 and September 2009 with epilithon after 3 weeks of in situ colonization. The maximum rate of the photosynthesis ($P_{max}$) correlated positively with the chlorophyll a content of the samples. Natural sites had lower biomass and $P_{max}$ values than modified sites, and the biomass differed substantially in spring and summer, the $P_{max}$ differed significantly only in spring. Natural sections had higher biomass-specific photosynthesis values than modified sections in all seasons, but the difference was significant only in summer-autumn: in summer the samples from the natural sections had significantly higher photosynthetic efficiency. In spring and summer, the photoadaptation parameters ($I_c$) of communities grown in modified sections were substantially higher than in natural sections. Light availability appeared to be the major factor regulating the seasonal photosynthetic activity of epilithic communities.

Keywords Epilithon · P–I characteristics · Torna-stream · Natural and modified sections · Riparian shading · Primary production

Introduction

Epilithon communities are very important primary producers in fast flowing running waters (Wetzel, 2001). In some streams, the major resource of the organic matter is provided by autochthonous primary production of periphyton rather than by the leaf fall of the terrestrial vegetation (Minshall, 1978). The importance of periphytic algae as primary producers was confirmed in many studies (e.g. Odum, 1956; McLastine & Phinney, 1965; Vannote et al., 1980; Busch & Fisher, 1981; Ostrofsky et al., 1998). These algae are consumed by aquatic macroinvertebrates (e.g. Mayer & Likens, 1987; Hansson, 1992; Lamberti, 1996; Munoz et al., 2001) and are often preferred to fallen leaves (Webster, 1983), serving therefore as major primary organic matter source of such food webs. Epiphytic algae are preferred indicators of water quality because of their sensitivity to environmental
parameters (Lange-Bertalot, 1979; Lowe & Pan, 1996; European Union, 2000). They are often used in biomonitoring for estimation of the ecological state of the aquatic environments (e.g. Vis et al., 1998; Gómez & Licursi, 2001; Gold et al., 2002; Maggs et al., 2004; Kovács et al., 2006; Kröpf et al., 2006).

The colonization begins immediately after a solid surface emerges into natural water, and the taxonomic composition and biomass of periphyton are affected by several physical and chemical parameters. Light is a major environmental parameter which influences biomass, taxonomic composition and primary production of benthic communities (Hill, 1996; Azim et al., 2005). Biomass and primary production of epiphyton is often affected by extent and patchiness of the riparian vegetation (Hill & Knight, 1988; Hill & Harvey, 1999; Elsegairi & Pozo, 1998; Ostrovsky et al., 1998; Figueroa-Nieves et al., 2006) and by the turbidity of the water body (e.g. Davies-Colley et al., 1992) which influences the amount of light reaching the periphyton (V-Balogh et al., 2009).

Removal of the riparian vegetation increases the importance of flood control which has an influence on the amount and composition of algal propagules (Uehlinger, 1991), and the concentration of major plant nutrients (e.g. Davies-Colley, 1990; Humphrey & Stevenson, 1992). Floods, moreover, influence the current velocity, and modify the geomorphology of the stream beds, the size and distribution of different substrates (Jowett & Duncan, 1990; Azim et al., 2005), and have an influence on the density of macroinvertebrates (e.g. Scrimgeour & Winterbourn, 1989; Quinn & Hickey, 1990; Opalsh et al., 2003), among them grazers. At increased velocities, the soft sediments are washed out from the spaces between the larger pebbles and stones, and as a consequence of continuous migration of the soft sediment, epipiemnmon and epipelon cannot establish (Azim et al., 2005), or their importance decreases contrary to the communities growing on hard, and stable substrates (Biggs & Shand, 1987). The increasing amounts of the suspended particles can shear the epiphyton from the substrate surface and cause an increase in water turbidity (Davies-Colley, 1990; Hill, 1996). Disturbances, such as floods or extended periods of high flow, may have a significant impact on periphyton biomass and metabolism (Uehlinger & Nuegeli, 1998).

Measuring the changes in the biomass of the different communities, the rate of the primary production is possible to estimate (e.g. Morin et al., 1999; Fellows et al., 2006), but simple measurements are often inappropriate to explore the ecophysiological responses of the communities to the changing light conditions.

Photosynthesis–irradiance (P–I) curves describe the short-term response of photosynthesis to changes in light intensity. Parameters of P–I curves depend on incident light, temperature and the structure of the autotrophic community (e.g. Gasseh & Sabater, 1995). Apart from some early studies (e.g. Odum, 1956; McIntire & Phinney, 1965), the number of the P–I measurements in running waters increased in the last two to three decades, but still lags behind the phytoplankton research. The two basic motives to measure the P–I relations are to (i) determine the ecophysiological responses to light, and (ii) predict in situ photosynthesis (Hill, 1996). The continuous development and innovation of the technical support and different methods (e.g. McIntire & Phinney, 1965; Hansmann et al., 1971; Steinman et al., 1990; Toth & Herodek, 2009) permit fast and sufficiently controlled measurements of the P–I characteristics and primary production. The parameters describing the P–I curve provide information on the physiology of the algae and variations in the parameters can reflect changes in environmental conditions (Falkowski, 1981; Falkowski & Raven, 1997; Sakshaug et al., 1997). Human activity can affect the environmental parameters, and consequently the metabolism of the autotrophic and heterotrophic organisms.

Recent photosynthesis research concentrates not that much on the primary production in itself but on its product, the biomass itself. Extent of primary production is important but even more important is the response of the ecosystem, for example, how the ratio of autotrophic and heterotrophic production changes to a given environmental forcing.

This study focused on the question of how seasons influence autochthonous primary production on the ecosystem level. Primary production was investigated in a small Hungarian stream that is characterized by sufficient nutrient concentrations, and includes sections with various riparian vegetation and bed morphology due to human activity. We assumed that modifications would have a significant impact on epilithic photosynthesis, and therefore expected to observe corresponding changes in P–I parameters. In the absence of riparian vegetation, P–I parameters and photosynthetic activity should be related to regular
seasonal changes. To test these hypotheses, we aimed to estimate the seasonal change of the biomass, the photosynthetic parameters, and the primary production of epilithic algal communities in modified and natural stream sections with different riparian vegetation of Torna-stream between April 2008 and September 2009 under laboratory conditions. In view of the former studies, we supposed that in some periods, especially in spring and summer, the photosynthetic activity of epilithon from modified sections without riparian vegetation might be higher, than those of the communities from natural stream sections.

Materials and methods

Study sites

Torna-stream, located in the western part of Hungary, is a small gradient (1–3‰) hilly stream with calcareous hydrochemistry flowing through a land formed on dolomite bedrock. Its length is 51 km and the catchment area is 498 km². The spring of the Torna-stream is located in the Bakony Forest (western part of the Transdanubian Midmountains). After collecting the water of three inflows (Csígeru-stream, Csinger-stream, Széles-víz), Torna flows into the Marcal River. The upper sections of the stream can be regarded as natural sections with dense riparian vegetation, where the streambed is covered by soft sediments and pebbles. From the town Ajka, the mid and downstream sections are heavily modified, the streambed is linear along long sections, shoreline is trapezoid and strengthened by concrete blocks; pebbles and larger stones occur on the streambed.

The study of the photosynthetic activity and biomass of epilithic algal communities of Torna-stream was carried out between April 2008 and September 2009. Two sampling sites were located at natural stream sections, Natural1 and Natural2; both situated near the village Csehúnyá (Bakony Forest). They did not differ significantly in water chemistry, current velocity, light availability and streambed morphology, and the average water depth varied between 15 and 35 cm. Two other sampling sites were located in modified stream sections; one of them was located between two villages, Kolontár and Devecser (Modified2); the other one in the inner area of the village Devecser (Modified1). The main difference between Modified1 and Modified2 was the irradiance measured at the bottom of the stream bed, but this difference was not significant. This difference of the light field is caused by the occasionally higher water turbidity because of the easier removable soil particles of the stream bank and the seasonal appearance of grass vegetation at Modified2 location. On the heavily modified mid and downstream sections, these two types of modified sections dominate and alternate. While the sections which are similar to the Modified2 location are more characteristic for populated areas, the sections which are similar to the Modified1 location dominate outside the populated areas. We expected the results be more representative by studying the all major and dominant types of the modified sections of the stream. The sampling locations are presented on Fig. 1.

Epilithon samples

For the P-I measurements, epilithon was grown on semi-natural bricks (commercially available natural freshwater limestone from a mine in Sütő, Hungary) with well-defined surface area (~25 cm²). The sides of the bricks were covered by paraffin, except one side, where the epilithon could grow (Fig. 2a, c). Sterilized bricks (30 per sampling site and per month) were fixed on a grid (Fig. 2b), which were exposed once a month. In experiments using sterile substrates, the length of the in situ incubation is very important (Reid et al., 1995). Initial colonization and development of maximal periphyton density typically lasts for 12–28 days (e.g. Murphy, 1984; Acs & Kiss, 1993; Kutka & Richards, 1996; Rier & King, 1996; Kelly et al., 1998; Uehlinger & Naegeli, 1998; Roman & Sabater, 1999; Barbiero, 2000; Cardinalet al., 2002; Lane et al., 2003; Bergey, 2005), therefore, the in situ incubation time was set as 21 days. After the in situ incubation, the bricks were removed from the sampling locations and were carried in dark to the laboratory for photosynthesis measurements. This procedure was repeated monthly between April 2008 and September 2009.

Field measurements

For each outplacement and sampling event, the light field at the sampling locations was measured with LI-SOSL spherical quantum micro sensor (Heinz Walz
Fig. 1. Sampling locations on the Torna-stream, Hungary. Natural sections both in the forest near to Csehbidnya: N1 Natural1, N2 Natural2; Modified sections: M1 Modified1, in Devecser; M2 Modified2, between Kocentir and Devecser.

Fig. 2. Semi-natural limestone substrates: a limestone bricks covered by paraffin, b substrates fixed on the grid, c limestone brick with periphyton on the not paraffinized side after 3 weeks colonization.

GmbH) connected to a data logger (LI-1400, Licor, USA). Light attenuation coefficient of the water column, k (m⁻¹), was calculated with the Lambert-Beer function (Kirk, 1994) from simultaneous measurements of light intensities in the field at time of samplings at two depths: the substrate surface and directly under the water surface. A continuous record of total daily global radiation, recorded at Széntkirályszabadja (30 km southeast from Csehbidnya) was provided by the Meteorological Service of Hungary. Knowing the global radiation data and vertical attenuation coefficient values, the light intensity reaching the stream bed was estimated. Daily light intensity (µmol m⁻² day⁻¹) at the surface of the substrates was calculated as the sum of the hourly light intensities from sunrise to sunset.

Water temperature was determined from simultaneous measurements in the field at the time of sampling at each sampling location (Fig. 3). There was no significant difference in the trend of temperature changes at the modified and natural sections of the stream, however, annual temperature range at the natural sections was narrower.

P-I measurements

The measurements were carried out in a laboratory incubation system, which was developed according to...
Tóth & Hercegá (2009) with a few alterations (Úveges et al., 2011). After the 3 weeks in situ incubation, the photosynthesis of the epilithic communities was measured every month in the laboratory at nine light intensities (0, 7.5, 30, 75, 150, 260, 500, 920 and 1320 µmol m\(^{-2}\) s\(^{-1}\) PAR), on the temperature measured in situ at the sampling site (Fig. 3). In every measurement, 3 bricks of the 30 removed from one sampling site were exposed to one particular light intensity, therefore, 27 bricks (9 light intensities \times 3 parallels) were included in one experiment. Exposure time was 2 h. The changes in the dissolved oxygen concentration were measured with the Luminescence Dissolved Oxygen (LDO) method (HQ40d, Hach Lange) every 30th minute during the 2 h. The photosynthetic activity of the samples was measured in most cases on the same day when the sampling was carried out but in any case within 24 h.

The limestone bricks were put into 600-ml glass beaker one by one with the colonized side upwards. The beakers were filled with 400 ml filtered (GF/C, Whatman International, UK) stream water collected at the sampling locations. Covering the medium with a transparent slide, the gas exchange between the medium and air was prevented. According to a preliminary study, there was no significant difference between the change of the dissolved oxygen concentration with or without stirring the medium (paired t test; \( n = 80; P = 0.693 \) at 95% confidence interval). Therefore, during the measurements the medium was not stirred.

The gross oxygen production was converted to carbon uptake (Westlake, 1966; Wetzel & Likens, 2000) and a software was applied to determine the P-I parameters (GnFit by R. Leatherbarrow, 1989-1992 Erimacrus Software Ltd.). The P-I parameters were calculated with the model by Webb et al. (1974) when photoinhibition did not develop. When photoinhibition was apparent in the P-I data, the P-I parameters were calculated with the model by Platt et al. (1980), because in that case the three-parameter model of Platt et al. (1980) is appropriate. The Platt et al. (1980) equation fits most photoinhibition data fairly well (Bill, 1996).

**Biomass**

After the photosynthesis measurements, the chlorophyll \( a \) and phaeophtyn \( a \) content of each of the samples was quantified. The pigments of the epilithon were extracted directly from the samples with 90% acetone. The direct extraction was used instead of brushing, because removing the epilithon from rough surfaces with worldwide applied brushing (Kelly et al., 1998; Steinman et al., 2006) might result the underestimation of the biomass (Palumbo et al., 1987; Beugy & Weaver, 2004). The chlorophyll \( a \) content corrected for phaeophtyn \( a \) was determined spectrophotometrically (Lorenzen, 1967; Tett et al., 1975; Wetzel & Likens, 2000), and it was normalized to the colonized surface area (mg m\(^{-2}\)).

**Statistical analysis**

Statistical analyses were performed using the R 2.7.2 software (R Development Core Team, 2009). Two-way ANOVA was used with season and sites as factors to test the presence of seasonal effects, differences between sampling sites and the interactions between the two factors. The post hoc comparison between individual sites and seasons was carried out by Bonferroni tests.

**Results**

**Biomass of epilithon**

There was no significant difference between the chlorophyll \( a \) values of sampling locations from the
same section type (Modified1 ~ Modified2: $t = 0.8021, df = 32.805, P = 0.4283$; Natural1 ~ Natural2: $t = -0.4411, df = 32.5, P = 0.6621$). The seasonal changes of biomass were different at sections with modified and natural riparian shading (Table 1).

The chlorophyll $a$ content of the epilithon at the Natural1 (3.4–31.7 mg m$^{-2}$; average: 22.9 ± 23.4 mg m$^{-2}$) and Natural2 (24.6–35.6 mg m$^{-2}$; average: 35.3 ± 19.2 mg m$^{-2}$) locations varied less, than at Modified1 (11.2–75.1 mg m$^{-2}$; average: 17.0 ± 9.2 mg m$^{-2}$) and Modified2 (10.2–87.9 mg m$^{-2}$; average: 15.8 ± 7.4 mg m$^{-2}$) locations. At each sampling location, the lowest chlorophyll $a$ content was measured in the winter months, the highest ones in spring and late summer (Fig. 4A). According to the post hoc comparisons, the chlorophyll $a$ content of samples was significantly lower in winter than in spring–summer both at natural and at modified sections. The chlorophyll $a$ content of the samples from modified sections were significantly higher only in the spring–summer period than that in natural sections (post hoc comparison with Bonferroni test). The low chlorophyll $a$ content (2.8–10.2 mg m$^{-2}$) of the samples collected in December 2008 at natural and modified sections and in January 2009 at the natural sections did not allow measurements of photosynthetic activity with the LDO method.

P-I characteristics

There was no significant difference between the maximum photosynthetic rate ($P_{\text{max}}$, mg C m$^{-2}$ h$^{-1}$) of communities from Modified1 (32.2 ± 17.2) and Modified2 (28.9 ± 14.7) locations ($t = 0.7889, df = 31.285, P = 0.4361$), furthermore between Natural1 (23.4 ± 6.5) and Natural2 (24.5 ± 7.5) sampling sites ($t = -0.4489, df = 29.371, P = 0.6568$). The $P_{\text{max}}$ was several times higher in the samples collected from the modified sections than in those from the natural sections (Fig. 4B), but the $P_{\text{max}}$ of modified section was significantly higher only in spring. According to the post-hoc comparison, the $P_{\text{max}}$ was significantly lower in winter than in spring and summer both at natural and at modified sections. At the sections without riparian shading the $P_{\text{max}}$ was significantly higher in spring than in other seasons. Only the spring difference was significant in post hoc comparisons between modified and natural sections. The seasonal changes in $P_{\text{max}}$ were different at sections with modified and natural riparian vegetation (Table 1). The $P_{\text{max}}$ correlated positively
Fig. 4 A Chlorophyll a content (mg m⁻²); B maximum photosynthetic rate, \( P_{\text{max}} \) (mg C m⁻³ h⁻¹); C biomass specific photosynthetic rate, \( P_{\text{max}}^{\text{m}} \) (mg C mg⁻¹ chl a h⁻¹); D photosynthetic efficiency, \( \alpha \) (mg C m⁻² h⁻¹ (μmol m⁻² s⁻¹)); E photopigment parameter, \( I_0 \) (μmol m⁻² s⁻¹) of epilithon communities collected from modified (Modified1, Modified2) and natural (Natural1, Natural2) sections of Torna-stream (Hungary) between April 2008 and September 2009 with the chlorophyll a content of the epilithon \( (r = 0.766, n = 72, P < 0.001) \) and with the in situ measured water temperature \( (r = 0.361, n = 66, P = 0.002) \).

There was no significant difference between the biomass specific photosynthesis \( P_{\text{max}}^{\text{m}} \) (mg C mg⁻¹ chl a h⁻¹) of communities from Modified1 \( (0.75 ± 0.25) \) and Modified2 \( (0.76 ± 0.75) \) locations \( (r = -0.0834, df = 31, 993, P = 0.934) \), furthermore between Natural1 \( (1.48 ± 0.61) \) and Natural2 \( (1.47 ± 0.69) \) sampling sites \( (r = 0.0289, df = 29, 56, P = 0.9771) \). The interaction between season and section was not
significant for $P_{\text{max}}$ (Table 1). Natural sections had higher $P_{\text{max}}$ values than modified sections in all seasons (Fig. 4C), but the difference was significant only in summer and autumn.

The photosynthetic efficiency, $\alpha$ (mg C m$^{-2}$ h$^{-1}$ (\textmu m$^{-2}$ s$^{-1}$)) of the communities from the Modified1 (0.161 ± 0.055) and Modified2 (0.142 ± 0.050) sampling sites did not differ significantly ($t = 1.0409$, df = 31.752, $P = 0.3058$). Between Natural1 (0.143 ± 0.036) and Natural2 (0.145 ± 0.034) locations, the difference of $\alpha$ was not significant ($t = -0.175$, df = 29.904, $P = 0.8622$). According to the post hoc comparison, the photosynthetic efficiency was significantly higher in the communities of natural sections only in the summer. In spring, the $\alpha$ value was remarkably higher at modified section than at the natural sections (Fig. 4D), but this difference was not significant. The seasonal differences of the photosynthetic efficiency were different at sections with modified and natural riparian shading (Table 1).

There was no significant difference between the photoproduction parameter ($I_{\text{p}}$, \textmu m$^{-2}$ s$^{-1}$) of communities from Modified1 (20-340 \textmu m$^{-2}$ s$^{-1}$; 226 ± 103) and Modified2 (19-342 \textmu m$^{-2}$ s$^{-1}$; 224 ± 103) locations ($t = 0.0393$, df = 32, $P = 0.9689$), and between Natural1 (39-250 \textmu m$^{-2}$ s$^{-1}$; 175 ± 58) and Natural2 (41-251 \textmu m$^{-2}$ s$^{-1}$; 177 ± 59) locations ($t = -0.0968$, df = 29.99, $P = 0.9235$). Seasonality was observed in the $I_{\text{p}}$ values both at the natural and the modified sections. The interaction between season and section was marginally significant (Table 1). In spring and summer, the $I_{\text{p}}$ values of the communities grown at modified sections were substantially higher than those of collected from natural sections (Fig. 4E), but this difference was significant only in the summer period (post hoc comparison). In spring and summer, higher $I_{\text{p}}$ values were measured (Modified sections average: 133-337 \textmu m$^{-2}$ s$^{-1}$; Natural sections average: 125-250 \textmu m$^{-2}$ s$^{-1}$) corresponding to the increasing incident light intensity. In autumn and winter, the amount of incident light decreased and caused lower community $I_{\text{p}}$ at each sampling location (Modified sections average: 20-219 \textmu m$^{-2}$ s$^{-1}$; Natural sections average: 40-217 \textmu m$^{-2}$ s$^{-1}$).

A drop of the photosynthetic activity was observed only at the highest applied light intensities in the communities of each sampling locations collected in November 2008 and January 2009, in that cases the occurrence of the photoinhibition was suspected. The photoinhibition parameter ($\beta$) varied between 0.003 and 0.006.

Primary production

Knowing $P_{\text{max}}$, $I_{\text{p}}$, hourly global radiation and vertical extinction coefficient ($k$), the primary production of epilithic communities was estimated for the studied period (Fig. 5). Summarizing the daily values, the monthly primary production was calculated for each sampling location. Most productive was the community grown in Modified1 location in May 2008 (>20 g C m$^{-2}$ month$^{-1}$). In spring and summer, the production of the communities from the modified sections was significantly higher than the production of communities from natural sections (spring: $F = 22.259$, $P < 0.01$; summer: $F = 96.103$, $P < 0.001$).

From April 2008 to September 2009, the summarized primary production could reach the 161.0 g C m$^{-2}$ at Modified1, 135.3 g C m$^{-2}$ at Modified2, 54.8 g C m$^{-2}$ at Natural1 and 56.9 g C m$^{-2}$ at Natural2 sampling locations.

Discussion

Methodology

Between April 2008 and September 2009, the photosynthetic activity of epilithic communities was measured monthly in laboratory using semi-natural limestone substrates for the colonization. The semi-natural substrates...
allowed for controlled colonization of epilithon on well-defined surfaces, and the measurements could be reproduced and repeated (Bergey & Getty, 2006). Because of the similarity of the substrate to the bedrock of the studied area, the growth rates of the communities allowed the nearest approach to the growth rates of communities grown on natural substrates (Kevan et al., 1966). Due to the moderate sensitivity of the LDO method at low chlorophyll levels, relatively high biomass was desired. The rough surface of limestone permitted the development of substantially higher biomass compared with smooth surfaces, like e.g. tiles (Godwin & Carrick, 2008). Covering the substrates with paraffin was an effective method to hinder the growth of algae on the bottom and lateral sides of the substrates (Fig. 2a, c).

The primary production was estimated in situ in open systems in many studies (e.g. LaPerriere et al., 1989; Parkhill & Gulliver, 1998; Bott et al., 2006; Uhlinger, 2006), from CO₂-flux or changes of O₂ concentration, but in these systems the gas exchange cannot be excluded (Bott et al., 1978). Closed chambers can be used both in situ and in laboratory (e.g. McIntyre et al., 1964; Hickey, 1988; Winterbourn et al., 1988; Munn & Bruaven, 2004; Uhlinger & Brock, 2005; Reid et al., 2006), and in these chambers either the oxygen (e.g. Ohman & Odum, 1955; Thomas & O’Connell, 1966; Hansmann et al., 1971; Lamberti et al., 1987; Dodd, 1992) or the radioisotope methods (e.g. Steffan-Nielsen, 1952; Riley, 1956; Grande et al., 1989; Ostrofsky et al., 1998) can be applied. The advantages of the laboratory measurements are the controlled conditions, the constant parameters while the irradiance varies, and the better reproducibility. With our incubation system, the photosynthetic activity of the communities could be measured at different light intensities and temperatures under laboratory conditions. The 2 h long laboratory incubation proved to be sufficient to the development of photoinhibition (Harris & Piccinin, 1977; Marr, 1978a, b; Macedo et al., 1998) without nutrient limitation would arise (Brock & Brock, 1967).

Epilithon biomass

The chlorophyll a content of the samples collected from the modified section was in all cases higher than in samples collected from the natural sections. The differences could be caused by the shading effect of the canopy cover at the natural sampling locations (Hill, 1996). In other experiments, investigating the effect of riparian vegetation on the epilithic biomass, a negative correlation between the density of riparian vegetation and the epilithic biomass was found (Hill & Knight, 1988; Hill & Harvey, 1990). Similar to results by Biggs (1995), we observed that the differences of the biomass between the modified and the natural sections were higher in late spring, summer and early autumn as in late autumn and winter. In the late autumn and winter months, the light availability was similar in both sections because of the lack of the closed canopy. Although the light availability of the modified sections was better, the chlorophyll a content (10.2–87.9 mg m⁻²) of the epilithic biomass was much lower compared with other streams with similar size and light field (e.g. Howard-Williams & Vincent, 1989; Boston & Hill, 1991; Biggs, 1995; Sabater et al., 2005; Figueras-Nieves et al., 2006; Godwin & Carrick, 2008; Kolmakov et al., 2008). However, in other small running waters with almost as good light conditions as in the modified section of the Tornaströmn even lower values were measured (e.g. Rout & Gaur, 1994; Pizarro & Vinocur, 2000). Compared with the chlorophyll a values (2.7–35.6 mg m⁻²) which were measured in the shaded section of the Tornaströmn there are streams where higher (Boston & Hill, 1991; Davies-Colley et al., 1992), and there are streams where lower values (Biggs, 1995) were measured. A number of reasons may explain these differences in biomass values in different streams with similar light conditions such as different current velocity, frequency of floods, the lack or presence of grazing macroinvertebrates, the size and amount of the suspended particles, etc. In streams with sufficient nutrient quantity, light is the major regulating factor (Hill & Knight, 1988; Hill et al., 1995; Hill, 1996). In the natural sections with closed canopy in the Tornaströmn also light was the limiting environmental parameter affecting most the epilithic biomass. The importance of the light intensity as regulating factor was shown by the seasonal changes of the biomass measured at the natural sections with dense riparian vegetation: the highest chlorophyll a values were measured in March similarly to Ostrofsky et al. (1998), when the amount of the incident light was higher because of the increased global radiation in spring and the undeveloped foliage. Increasing of the biomass in stream sections with riparian vegetation can be measured before the development of the foliage.
or after the autumnal leaf fall. A creek in Illinois is a
good example for the autumnal biomass peak (Figue-
roa-Nieves et al., 2006), but in our study it was not
characteristic at the natural sections presumably
because of the lower water temperature and decreased
global radiation (Phinney & McIntire, 1965; DeNic-
ola, 1996; Sabater et al., 2005; Godwin & Carrick,
2006). Similarly to Rosenoud (1994) and Eloségui &
Porz (1998), the seasonal changes of the biomass in
natural sections during the experimental period were
not as remarkable as in modified sections because the
seasonal change of the foliage and the amount of light
reaching the stream bed was more balanced. In winter
periods, not only the decreased light intensity, but also
the substantially lower temperature contributed to
development of significantly lower biomass compared
with the spring and summer periods.

At the modified sections, the seasonal change of the
biomass was more remarkable than at the natural
sections, which could reflect the physiological adap-
tation of the epilithon communities to the highly
variable parameters (Sand-Jensen et al., 1988; Yang
et al., 2009). Like in other studies (Kjeldsen et al.,
1996; Stevensen et al., 2006), Cladophora sp. appeared
on the surface of the substrates at the modified sections
in the summer period, which could be expected
because of the increasing water temperature and
because of the sufficient nutrients, but it could not
reach remarkably higher biomass during the 3 weeks in
situ incubation period. Diatom species were dominant
in the samples during the whole experimental period.

In the samples from the natural sections: Navicula
tripunctata, Anomala veneta and Achnanthes sp.,
and in the samples from the modified sections:
Navicula lanceolata, Gomphonema ollivareum, Frazil-
aria capucina var. vaucheriæ, Cocconeis placentula
and Achnanthes minutissima were dominant.

P-I characteristics of epilithon communities

The maximum photosynthetic rate ($P_{\text{max}}$) correlated
positively with the incident light intensity ($r = 0.792$;
n = 66; $P < 0.0001$) and with the water temperature,
but the positive correlation between $P_{\text{max}}$ and tempera-
ture was less pronounced ($r = 0.361$; n = 66; $P = 0.0229$).
Because of the strong positive correlation
between $P_{\text{max}}$ and biomass, the changes of the
$P_{\text{max}}$ were similar to the changes of the biomass
between the different seasons. Similarly, strong
positive correlations were observed between $P_{\text{max}}$
and chlorophyll $a$ content of epilithon communities
in other studies (Ertl & Tomajka, 1973; Davies-Colley
et al., 1992; Kolmakov et al., 2008). The $P_{\text{max}}$ at the
modified sections with better light availability was
significantly higher only in the spring than at the
shaded natural sections. The seasonality of $P_{\text{max}}$ was
observed only at the modified sections, until the
riparian vegetation balanced the seasonal changes of
$P_{\text{max}}$ at natural sections. Unfortunately, the photosyn-
thetic activity was not measurable with the LDO
method, not only because of the low biomass, but also
because of the decreased activity caused by the low
winter temperature.

The parameter provides information about pho-
tosynthetic efficiency at the lower range of light
intensity. The photosynthetic efficiency at locations
and periods with lower light availability was higher
than in samples collected from locations or in periods
with higher light intensities. Periphyton grown under
low light intensities responds fast to small incremental
increase of light intensity in many cases, and therefore
can reach the maximum photosynthetic rate at rather
low light intensities. McIntire & Phinney (1965)
observed a similar result in their experiment where
periphyton were grown at 40 and 110 $\mu$mol m$^{-2}$ s$^{-1}$
light intensities: the photosynthetic efficiency of
periphyton grown at 40 $\mu$mol m$^{-2}$ s$^{-1}$ was higher,
but $P_{\text{max}}$ and $I_{\text{d}}$ were lower, than those of periphyton
grown at higher light intensity. In another study, the
photosynthetic efficiency was substantially higher in
communities grown at the shaded sections of a stream
(50 $\mu$mol m$^{-2}$ s$^{-1}$) than at the sections with better
light availability (1100 $\mu$mol m$^{-2}$ s$^{-1}$) (Hill et al.,
1995). Within natural conditions, the communities
grown in shaded sections cannot reach as high
photosynthetic activity as in sections with increased
light availability, since in shaded sections the light
intensity is insufficient to reach the $P_{\text{max}}$ (Hill et al.,

Epilithon communities had lower biomass when the
samples were collected from sections and in periods
with low light. Because of their higher photosynthetic
efficiency, their light utilization was in many cases
higher than in communities developed at sections and
in periods with high light availability. As in other
studies, the biomass-specific $P_{\text{max}}$ correlated nega-
tively with the biomass of the community (Pfeiffer &
McDiffett, 1975; Sumner & Fisher, 1979; Morin et al.,
In the biomass-specific photosynthesis ($P_{\text{max}}^b$), there was no difference in the seasonality between the modified and natural sections. Natural sections had higher $P_{\text{max}}^b$ values than modified sections in all seasons, but the difference was significant only in the summer, when the samples from the natural sections had significantly higher photosynthetic efficiency.

The riparian vegetation affected the photoadaptation of the epilithon, too. The photoadaptation parameter, $I_0$, of the communities did not differ significantly between the modified and natural stream sections in the cold period because of the similar light environment after the leaf-fall. In the spring and in the summer, however, the $I_0$ of communities grown in modified sections were substantially higher than in natural sections, but this difference was significant only in the summer period as observed in other studies (Boston & Hill, 1991; Hill et al., 1995).

Photoinhibition was observed only in communities collected in late autumn and in winter. When benthic algae from shaded habitats are exposed to relatively high irradiances (e.g. >1000 μmol m$^{-2}$ s$^{-1}$), they often experience much more photoinhibition than algae from habitats with better light availability (Boston & Hill, 1991). Hill et al. (1995) hypothesized that some of the sensitivity of shaded algae to photoinhibition in laboratory measurements was due to low levels of light-shielding accessory pigments. In our study, the appearance of photoinhibition was assumed in these samples, where a drop of photosynthetic activity was observed at higher light intensities (Han et al., 2000). The damage of the photosynthetic apparatus after the measurements were not examined therefore we have no information, if the decline in photosynthetic activity was due to irreversible damage of the photosynthetic apparatus.

In other seasons with higher incident light photoinhibition did not develop. The reasons could be (1) the communities grown under high light conditions could adapt to the higher light intensities, with more accessory pigments in their photosynthetic antenna system (Hill, 1996); (2) during the 2 h incubation the photoinhibition could not develop, but according to Palkowski (1984) this time is enough for its development; (3) the applied light source might provide less radiation in the shorter wavelength range (Vincent & Roy, 1993); (4) the epilithon might have been so thick, that the lower layers could compensate the photoinhibition of the upper layers (Sand-Jensen & Revsbech, 1987).

Primary production

Differences can be observed between the natural and the experimentally measured primary production (Fellows et al., 2000) because of (1) the presence of grazing macroinvertebrates (Murphy, 1984; Lamberti et al., 1987; Steinman, 1996; Wellnitz & Ward, 2000; Hillebrand & Kahler, 2001), (2) changes of the flow velocity (McIntire, 1966; Horner et al., 1990; Cardinale et al., 2002; Villeneuve et al., 2010), (3) activity of bacteria (Fukuda et al., 2006) and (4) the photosynthetic parameters were determined after 3 weeks of in situ incubation, but the natural mature epilithon might be much older. Despite the shortcomings of the estimation of the primary production, the role of the epilithon communities in the nutrient and energy flux is undisputed. The streambed is covered by rocks and pebbles on the majority of the stream. In lack of phytoplankton, the epilithon communities are the most important primary producers of the Torna-stream. These communities provide an important food source for grazing macroinvertebrates (Webster, 1983) and for bacteria (Lock & Hynes, 1976), which prefer autochthonous organic matter instead of fallen leaves. This way the epilithon communities could have a more important role at the natural sections of the Torna-stream in context to their low biomass and the remarkable allochthonous load of organic matter (Chapman & Demory, 1963; Ostrofsky et al., 1998).

The results suggested that light availability was the major factor regulating the seasonal photosynthetic activity of epilithic communities. The dense riparian vegetation was able to mitigate the presence of a seasonal effect on the epilithon biomass and metabolism. The observed variation in $P_{\text{max}}$ characteristics may be explained mainly by the adaptation of epilithon to the changing light and temperature conditions.

Epilogue

On 4 October, 2010 Hungary’s most serious industrial disaster occurred. About 10$^6$ m$^3$ alkaline (pH close to 13) sludge escaped from an aluminium plant reservoir and the red sludge flood reached the modified section of the Torna-stream, including sampling sites named Modified1 and Modified2 in this article. All living organisms were killed downstream the catastrophic
there are little, if any, signs of regeneration at the time of the manuscript submission. Data in this article as well and other information from the same sites will be essential for monitoring the regeneration serving as a good benchmark of the future conditions.

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