

The effect of periphyton on the light environment and production of *Potamogeton perfoliatus* L. in the mesotrophic basin of Lake Balaton

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Abstract

Light within the littoral zone affects the productivity and interaction between periphyton and its macrophyte substrate. The effect of periphyton on macrophyte photosynthesis, seasonal variation and vertical distribution of periphyton on artificial substrates (plastic strips), and the effect of periphyton on the light environment was studied in Lake Balaton.

Data showed that an average of 4.1 ± 0.4 mg (dry weight) cm^{-2} of periphyton had accumulated on the plastic strips after 8.8 ± 0.4 days. This biomass corresponded to 294 ± 30 $\mu\text{g m}^{-2}$ chl-a of epiphytic algae and blocked 92.3 ± 0.8 % of the depth specific radiation.

Seasonal variation and specific vertical distribution of periphyton were observed. The most active time of periphyton accumulation corresponded to spring up until mid-June. Later in the year, the amount of periphyton significantly decreased. The optimal conditions for periphyton accumulation were at 30-40 cm depth.

Most of the light reaching the adaxial leaf surface was attenuated by periphyton, decreasing the production of *Potamogeton perfoliatus* by 60-80%. This increased the importance of backscattered light that corresponded to 10-15% of the macrophyte production.

A smaller part of the periphyton consisted of precipitated inorganic material, while epiphytic algae, making up the majority of the periphyton, were connected to both benthic (dominantly

benthic penaeles) and pelagic (very close seasonal dynamics of pelagic and epiphytic biomass) algae. Periphyton affects macrophyte production especially in spring and in the upper water layers even in a mesotrophic water body. This increases the importance of the light absorbed through the abaxial side of the leaf and confirm the role of periphyton in transition from clear to turbid water states.

Keywords: periphyton; vertical distribution; seasonal change; macrophyte production; Lake Balaton; Potamogeton perfoliatus

Introduction

Understanding community assembly of the littoral zones of freshwater lakes is one of the major goals of limnology. Complex interactions between submerged macrophytes, associated periphyton and phytoplankton increase their ecological significance in maintaining the water clarity of lakes (Becares et al. 2008; Jeppesen et al. 1997; Jones and Sayer 2003; Scheffer et al. 1993; Vis et al. 2007). Since primary producers depend mainly on light availability, they are in constant competition for this resource (Becares et al. 2008; Jones et al. 2002; Jones and Sayer 2003; Roberts et al. 2003; Weisner et al. 1997). The reduction of available light associated with an increase of planktonic and epiphytic algal content could result in the decline of submerged macrophytes and thus a significant reduction in biodiversity (Blindow et al. 1993; Scheffer et al. 1993). On the other hand, macrophytes, through increasing the amount of the plant associated with macroinvertebrate and fish populations (Jones and Sayer 2003; Stephen et al. 1998), and via allelopathic suppression (Gross 2003), can affect both periphyton and plankton community structure and size.

The unidirectional property of light and its exponential extinction within the water column results in a very specific, vertical competition for light (Hill 1996; Kirk 1994). Biotic and abiotic light attenuation strongly influences the availability of light in the lower regions of the water column, and thus has a substantial impact on all autotrophic organisms and their community structure (Bécares et al. 2008; Jones and Sayer 2003; Liboriussen and Jeppesen 2009). Periphyton, due to its high epiphytic algae content, is also influenced by changes in light attenuation (Jones et al. 2002; Lalonde and Downing 1991; Müller 2006), while negatively

impacting both phytoplankton (Trochine et al. 2011) and the plant substrate (Bécares et al. 2008; Jones and Sayer 2003).

Water turbulence periodically allows phytoplankton to reach the well-lit areas of the water column (Litchman and Klausmaeier 2008; Reynolds 1994), while sessile periphyton must adapt to the light environment of the given depth (Brandt and Koch 2003; Liboriussen and Jeppesen 2009) and compete with phytoplankton when light is limiting (Hansson 1992). On the other hand, chlorophyll content and thickness of the epiphytic layer (Dodds et al. 1999; Enríquez et al. 1996) leads to a competitive interaction for light between periphyton and its macrophyte substrate (Bécares et al. 2008; Jones and Sayer 2003). Thus, the specific depth distribution of epiphyte biomass directly influences light capture efficiency, morphology and physiology of macrophytes by additional attenuation of light at the adaxial side of leaves (Asaeda et al. 2004; Sand-Jensen and Borum 1991; Sultana et al. 2010). Macrophytes also affect periphyton. Macrophyte morphotypes differing in architecture, leaf type, lifespan of leaves, vertical biomass distribution, etc. have a significant influence on the accumulation of periphyton, and the biomass and depth distribution of epiphytes (Nöges et al. 2010; Romo and Galanti 1998). The interaction between macrophytes and epiphytes varies not only spatially, but over time with the growth and succession of both macrophytes and algae (Wetzel 1975).

Light is a crucial factor for submerged rooted macrophytes (Abernethy et al. 1996; Bowes and Salvucci 1989; Goldsborough and Kemp 1988; Sabbatini and Murphy 1996) and its biotic and abiotic attenuation is responsible for morphological (shade-tolerance) and architectural (shade-avoidance) modifications of plants with the aim of enhancing the capture of radiation (Pilon and Santamaria 2002; Tóth et al. 2011; Vári et al. 2010; Wolfer et al. 2006).

Physiological acclimation to a given environment does not always follow this trend (Tóth et al. 2011), although reports show successful acclimation to the light environment in other species (Maberly 1993; Spence and Chrystall 1970). This natural pattern of vertical within-plant variability could be heavily influenced by epiphytic light attenuation, thus it is important to know more about the vertical distribution of periphyton and the resulting influence on the production of macrophyte substrate.

The impact of periphyton on production of *Potamogeton perfoliatus* was studied in the mesotrophic, thus macrophyte-dominated clear-water basin of Lake Balaton. The effect of the periphyton was estimated through its light quenching and consequent effect on macrophyte production. It was assumed that periphyton would significantly influence the light capture capability of *P. perfoliatus*. Based on this assumption, vertical distribution, seasonality and colonisation dynamics of periphyton, and its effect on the photosynthesis of *P. perfoliatus* was studied.

Materials and Methods

Lake Balaton

Lake Balaton is a large (596 km²) and relatively shallow (average water depth 3.5 m) lake. The lake is 77 km long and 5.5 km wide on average, stretched along a predominant southwest-northeast axis that is perpendicular to the prevailing, north-north-eastern winds of the region. This results in the distinctive nature of its northern and southern shores: the sediment of the windward, steep northern shore, more protected by mountains, consists of dolomite limestone, while the shallow, more wind-exposed, southern shore is dominated by sandy sediment. In addition to this striking north-south difference, there is also a west-east trophic gradient due to the only large inflow into the lake at its westernmost basin. This results in a eutrophic westernmost and a mesotrophic easternmost basin in Lake Balaton.

Periphyton experiments

In preliminary experiments, nine transparencies were examined for their optical homogeneity (between 320 and 800 nm), flexibility, and overall likeness to the surface of the *Potamogeton perfoliatus* leaves. APLI transparencies (Ref. 01495, APLI, Spain) were chosen. These preliminary experiments showed that the variability of periphyton accumulation at the same depth is low, that horizontal strips accumulated more periphyton (>95%) on the upper surface, and that the periphyton on the strips was saturated after ca. 10 days (following day 10, a very low (<7%) increase in periphyton biomass was still observed).

For field experiments, a site near the Balaton Limnological Institute was chosen (N: 46°54'50.53", E: 17°53'37.60"). The experimental setup was arranged in front of a rocky shore, in a wave exposed area, close to a *P. perfoliatus* stand. At this site, the sediment is a mix of large stones and manganese rich calcite sand.

Experiments were performed between March 22 and October 9, 2010. To model *P. perfoliatus* of Lake Balaton, plastic strips 44 mm long and 14 mm wide (~6.2 cm²), representing the average size of *P. perfoliatus* leaves on the northern shore of Balaton (Tóth et al. 2011; Vári et al. 2010), were cut from APLI transparencies. The plastic strips were weighed and attached horizontally to a fishing line at seven predefined positions, 20 cm apart, with three strips at each depth. Five fishing lines were prepared as such, and each fishing line was fixed to a metal pole emerging 30-40 cm above the water surface, held by ballasts at the other end (Fig. 1).

All five fishing lines were placed into Lake Balaton, with the upper set of strips at the water surface, at a 1.4 meter deep site, close to the shoreline. Every first, third, sixth, eighth and tenth day of each experiment, one fishing line was removed. After the final sampling (day 10), the experiment was restarted with a frequency of once every second week.

In the laboratory, the optical properties of the plastic strips were measured in precision cuvettes made of optical glass (№710/5, Assistent, Germany) using a spectrophotometer (UV-VIS 1601, Shimadzu, Japan). Transmission, reflectance and absorption spectra of each plastic strip in an empty cuvette were recorded between 800 and 320 nm, with 1 nm wavelength bandwidth. Later, a plastic strip was used for chlorophyll measurement following the 90% acetone method (Ritchie 2008), and the dry weights of the remaining strips were determined.

Validation experiments

Periphyton accumulation on the plastic strips was compared with periphyton biomass on *Potamogeton perfoliatus* leaves grown near the experimental site and in similar condition (depth, wave exposure, etc.). To ensure a full accumulation of periphyton on the apical parts of plants, fully matured (reaching the surface of the water for at least two week) *P. perfoliatus* were used. Validations were performed every fortnight starting from 20 June (07/20, 08/03 and 08/17) at the time of the

final sampling of the plastic strips (day 10; see Periphyton experiments section above). Mature, intact leaves from the same depths at which the plastic strips were placed (see above) were carefully collected from four plants and transferred into 20 ml vials filled with distilled water. In the laboratory, the vials were shaken to remove periphyton from the leaves, and the resuspended periphyton was filtered onto previously dried and weighed GFC (Whatman, USA) filters. Filters were dried at 60 °C for one week and then weighed again. The *P. perfoliatus* leaves, forming the substrate for periphyton, were scanned and later processed to determine the area of each leaf using ImageJ software (version 1.36, <http://rsb.info.nih.gov/ij/>).

Light measurements

At the experimental site, eight pendant temperature and light sensors (Onset Computer Corporation, USA) faced upward, measuring downwelling irradiance; one just above the water surface and seven every 20 cm deeper). Four sensors (at 0, 40, 80 and 120 cm depth) faced downward, measuring upwelling irradiance. The opposite side of all sensors was covered with black plastic to ensure the detection of the radiance from only one direction. Any periphyton was removed from the sensors at the start of each experiment (every fortnight). The sensors used are 2π light sensors measuring light intensity in Lux, and were intercalibrated with a spherical irradiance sensor (US-SQS/L, WALZ, Germany) attached to a data logger (LI 1400, LI-COR Biosciences GmbH, Germany) at all depths.

Photosynthesis measurements

Close to the experimental site (<3 m), at a depth of ca. 1.5 meters, 9 intact, healthy looking *P. perfoliatus* plants were collected for photosynthesis measurements once a month between April and October 2010. In the laboratory, two fully mature leaves were collected from the apical and basal part of each plant. Collected leaves were used for photosynthetic measurements in a tank (Tóth and Herodek 2009). Filtered (Whatman, GFC, poresize 1.2 μ) lake water filled 300 ml Karlsruhe vials (WTW, Germany) had a leaf in each. These were placed into

an incubation tank illuminated with five fluorescent tubes (F33 Coolwhite, Tungsram, Hungary, correlated colour temperature 4000K) from both sides. For light quenching, RE50NEARL Scotchshield™ Ultra Safety and Security Window film (3M, USA) was applied in varying thicknesses to specific areas of the incubation tank, resulting a range of light intensities (18, 43, 113, 205, 408 and 780 $\mu\text{mol m}^{-2} \text{s}^{-1}$) (Tóth and Herodek 2009). Irradiance was determined using a spherical irradiance sensor (US-SQS/L, WALZ, Germany) attached to a data logger (LI 1400, LI-COR Biosciences GmbH, Germany). The temperature of the incubation tank was set to the actual water temperature of Lake Balaton with a cooling-heating bath (Neslab RTE-17, Thermo Electron, USA). Mixing was provided by stirring bars and specially made magnetic stirrers (Tóth and Herodek 2009). Photosynthesis and dark respiration was measured using an oxygen electrode connected to a data logger (TriOxmatic 300 and Oxi 539, WTW, Germany), with 30 minute dark incubation and 30 minute light incubation times. The pH of the incubation water was measured at the beginning and end, while DIC was measured at the time of sampling and at the end of photosynthesis measurements. Changes in pH and DIC were less than 1%.

Mathematical and statistical data analysis

The photosynthesis–irradiance (PI) data were fitted with an exponential saturation model (Webb et al. 1974): $P = R_d + P_{\max} \cdot (1 - e^{-I/I_k})$. Macrophyte production was also calculated from the Webb equation using irradiances (I) collected by pendant temperature and light sensors at different depths throughout the vegetation period (and then corrected by the determined light attenuation of the periphyton), the measured dark respiration (R_d), saturation photosynthesis (P_{\max}), and theoretical saturation irradiance (I_k) from the fit. The compensation irradiance was also calculated from the fitted data according to the following equation:

$$(I_c = I_k \cdot (-\ln[1 - R_d/P_{\max}])).$$

To describe the sigmoid saturation dynamics of periphyton accumulation, a three parameter logistic equation ($y = a/(1 + [x/x_0]^b)$) was fitted to the dry weight data of the first, third, sixth, eighth and tenth days. The saturation parameter of the logistic function (b) was used to describe the biomass saturation dynamics.

It was obvious that all the measured periphyton traits showed a peak at a certain depth. To estimate the peak in the depth distribution of the studied parameters, all data from the same depth were pooled and a three parameter Lorentzian function ($y = a/(1 + [(x - x_0)/b]^2)$) was fitted to the chl-a, transmittance and periphyton biomass data.

Sigma Plot v 8.0 (Systat Software Inc., USA) was used to graph results and for curve fitting. The fit of all functions were checked with ANOVA. A Principal Component Analysis was performed (with data standardized by its standard deviation), adding convex polygons afterwards to picture potential patterns, using RExcel v.3.2.0. For differentiation between seasonal data, a t-test was used. For correlating data, Spearman correlation was used. Normality and homoscedascity were determined and when necessary data were transformed to attain a normal distribution. RExcel v.3.2.0. (Baier and Neuwirth 2007) was used for statistical analysis.

Results

Periphyton experiments

Accumulation of periphyton on the surface of plastic strips, the epiphytic algal chlorophyll-a, and light transmittance through the strips showed a significant seasonal and strong vertical pattern (Fig. 2). Based on these traits, Principle Component Analysis identified two distinct temporal groups (Fig. 3) in the vegetation period: spring (up to mid-June) and summer-autumn. The beginning of the vegetation period (till mid-June) had very low transmittance (ca. 1.5%) due to high periphyton biomass (ca. 7 mg cm^{-2}) and consequently high chl-a content of the epiphytic biofilm (ca. $470 \text{ } \mu\text{g chl m}^{-2}$), while the summer-autumn periphyton and epiphytic chl-a content was significantly lower ($\sim 2 \text{ mg cm}^{-2}$ and $160 \text{ } \mu\text{g chl m}^{-2}$), resulting in a relatively high transmittance (13%) (Table 1). This distinct seasonal variation did not affect the dynamics of periphyton accumulation: the plastic strips were saturated on day 9.5 ± 0.4 and 8.4 ± 0.4 of the experiment, respectively (Table 1).

A definite vertical pattern was observed; periphyton had higher biomass in the surface waters (20 to 80 cm) where it occasionally reached as high as 22 mg cm^{-2}

(Fig. 2b). Seasonal average (all data throughout the season at the same depth) showed maximum periphyton accumulation at 43 cm deep water (Fig. 2a). The correlation between periphyton biomass and transmittance was significant ($y=83.8e-1.72x$, $R=0.93$, $P<0.001$, data not shown), resulting in a strong vertical pattern with a minimal transmittance at depth of 38 cm ($2.7\pm 1.3\%$, Figs 2c and 2d).

Chlorophyll of the accumulated periphyton on plastic strips also showed distinct seasonal (Figs 2f and 4, Table 1) and vertical (Fig. 2e) distributions. Chlorophyll content was very high in spring and early summer ($489\pm 64 \mu\text{g chl m}^{-2}$), but later in the season it decreased to only $139\pm 17 \mu\text{g chl m}^{-2}$ (t-test $t=5.3$, $P<0.001$) (Fig. 2 and Table 1). A depth distribution of epiphytic chlorophyll-a content was also apparent (Figs 2e and 2f) with maximum chlorophyll content at a depth of around 30 cm (Fig. 2e). The relative contribution of chlorophyll accumulation to periphyton biomass accumulation and light quenching was not always uniform: until biomass reached $1.5 - 2 \text{ mg cm}^{-2}$, there was no detectable or statistically significant chlorophyll on the surface of plastic strips. Later, the increase of biomass on the surface of plastic strips was significantly correlated with an increase in chlorophyll concentration of the film ($y=78.6x$, $R=0.66$, $P<0.001$, data not shown).

Validation experiments

The biomass of periphyton on plastic strips correlated significantly (between 0.82 and 0.89; with at least $P<0.02$) with periphyton on *Potamogeton* leaves (Fig. 5). The biomass of periphyton on plastic strips was lower (on average ~50%) than on plant leaves, although this difference became significant only at 100 and 120 cm depths (t-test, $t=-6.5$, $P=0.001$ and $t=-3.8$, $P=0.012$, respectively) (Fig. 5). Nevertheless, the vertical pattern in biomass distribution on plastic substrates was strongly correlated ($y=0.45x$, $R=0.94$, $P=0.002$) with the biomass accumulation on natural substrate (Fig. 5, inlay graph).

Light measurements

High light attenuation of epiphyton (Figs. 2c and 2d, Table 1) enhanced the importance of the upwelling irradiance backscattered from the suspended solids in

the water column (Fig. 6). The relative importance of upwelling irradiance (as a % of the epiphyte quenched downwelling irradiance) was higher in spring and early summer, reaching its maximum (600%) in the second half of May at 40 cm depth (Fig. 6). Starting from mid-June, significance of the upwelling irradiance decreased and varied between 4 and 38% with no specific vertical distribution (Fig. 6).

Photosynthesis measurements

The maximum intensity of *P. perfoliatus* photosynthesis (P_{\max}) during the vegetation period varied between 4.6 and 13.4 mg O₂ g⁻¹ h⁻¹ (Fig. 7) and showed a strong, positive correlation with both sampling date and water temperature on the day of sampling (all $R > 0.51$, all $P < 0.05$). The intensity of dark respiration (R_d) decreased from 3 in spring to 2 mg O₂ g⁻¹ h⁻¹ in the middle of summer, and was followed by another increase to 3.4 mg O₂ g⁻¹ h⁻¹ in September (Fig. 7). The compensation irradiance (I_c) of *P. perfoliatus* during the vegetation period varied between 16 and 25 μmol m⁻² s⁻¹ without temporal or thermal correlation (Fig. 8), while the theoretical saturation irradiance (I_k) of plants significantly increased from 83 in spring to 204 μmol m⁻² s⁻¹ in late summer (Fig. 7), showing a strong, positive and significant correlation both with the date of the experiment and water temperature on the day of sampling (all $R > 0.81$, all $P < 0.001$).

Photosynthesis of *P. perfoliatus*, defined predominantly by downwelling irradiance (without epiphytic light quenching), shaped the potential production of *P. perfoliatus* in the mesotrophic basin of Lake Balaton, which was on average 117±7 mg O₂ g⁻¹ d⁻¹ (seasonal average), with substantially lower photosynthesis in the early months of the vegetation period, compared with after July (Fig. 8a).

Periphyton reduced the irradiance to reach the adaxial surface of leaves, thus decreasing the production of pondweeds by 90% to 13±4 mg O₂ g⁻¹ d⁻¹ (Fig. 8b). With backscattered, upwelling irradiance, the production increased to 26±5 mg O₂ g⁻¹ d⁻¹, with an additional increase in seasonal differences (Fig. 8c). In the first half of the vegetation period, production of pondweeds showed little vertical variation and was between 0 and 35 mg O₂ g⁻¹ d⁻¹. Production of *P. perfoliatus* was highest in July and August: the production in the upper 20 cm of the water column

reached 125-250 mg O₂ g⁻¹ d⁻¹, while lower in the water column, the daily production was under 70 mg O₂ g⁻¹ d⁻¹.

Discussion

The distinctive and diverse community of autotrophic organisms of the littoral zone (macrophytes, epiphytic algae and phytoplankton) is the important trophic base of the food web in freshwater lakes. Understanding the complex interactions between the components is an important task of limnology.

Periphyton can affect macrophytes through various mechanisms, such as nutrient and carbon competition, allelopathy, hosting grazers, etc. Previous studies showed that the amount of nutrients (nitrate and phosphorus) in sediment pore water is sometimes 2-3 order higher than in open water, thus rooted macrophytes are more likely to take up these elements from the sediment (Barko and James 1998; Sand-Jensen 2008). Competition for carbon can play an important role, especially in dense macrophyte patches, where water movement is limited (Sand-Jensen and Borum 1991). In Lake Balaton, intense water turbulence increases the dissolved inorganic carbon content of the water while decreasing the boundary layer diffusive limitations for carbon uptake by macrophytes, thus it is only of local (behind peers and reed stands) importance (Herodek et al. 1988).

Allelopathy, in general, is considered to have an effect on macrophytes (Gross 1999, 2003) and periphyton (Van Donk and de Bund 2002). In our experiments, the biomass of epiphytes on *P. perfoliatus* leaves were ~50% higher than on plastic strips, suggesting no allelopathic effect of epiphytes on macrophytes. Thus, the only effect periphyton can exert on macrophytes would seem to be shading. Light is a crucial factor for all submerged rooted macrophytes and defines the depth limitation of their survival. Traditionally, the maximum depth of penetration of rooted, submerged macrophytes is considered to depend mainly on water turbidity (e.g. Chambers and Kalff 1985; Jørgensen et al. 1997, Scheffer and Nes 2007), shading effects of plankton and epiphyte biomass (Bécares et al. 2008; Liboriussen and Jørgensen 2009; Scheffer et al. 1992; Sand-Jensen and Borum 1991; Strand and Weisner 1996).

Periphyton

Results of the study showed that periphyton accumulation significantly reduced the amount of light reaching the adaxial surface of the plant. This decreased amount of light diminished the production of *Potamogeton* plants, which could lead to decreased growth of these plants as described in previous studies (Bécares et al. 2008; Liboriussen and Jørgensen 2009). Light attenuation of periphyton was the consequence of intense accumulation of both resuspended inorganic material and epiphytic algae, but this accumulation was not uniform through the season. Epiphyte accrual was highest in the beginning of the vegetation period, while from mid-June, periphyton biomass decreased. Similarly, high epiphyte biomass was measured in the beginning of the vegetation period by others (Cattaneo et al. 1998; Gross et al. 2003; Nøges et al. 2010; Vis et al. 2006), while in other lakes, the production maximum usually appears later (Cattaneo and Kalff 1980; Nøges et al. 2010).

Seasonal variation of epiphyte biomass has already been discussed (Cattaneo and Kalff 1979, 1980; Wetzel 1975) and was demonstrated to be controlled mainly by the composition of the epiphytic algal community (Bécares et al. 2008; Liboriussen and Jørgensen 2009). Our results suggest that this seasonal difference could be attributed to the increase in water temperature in June. Weather conditions in May 2010 (stormy and very cold) postponed the seasonal shift in pelagic phytoplankton composition with Heterokontophyta (mostly Bacillariophyceae and primarily centric diatoms) dominating in the spring (Présing et al. 2001; Présing et al. 2008; Présing 2011). The decrease in epiphyte biomass in mid-June coincided with the end of the spring peak in pelagic phytoplankton diatom content, suggesting the role of Bacillariophyceae in the development of epiphyte cover. The influence of temperature on algal community composition is in accordance with other results from shallow lakes throughout Europe (Bécares et al. 2008). Although not the goal of the current study, microscopic analysis of the periphyton showed the dominance of benthic, mainly pennate diatoms (Kovács 2011). This strong temporal and probably causal synchronicity of pelagic and epiphytic algae suggests their tight interaction in the process of lake eutrophication. The increase in nutrient content of the water shifts lakes from clear water (macrophyte governed) to a turbid (algae dominant) state,

not directly via the shading effect of phytoplankton (Scheffer et al. 1992; Weisner et al. 1997), but rather through light attenuation by the increased biomass of epiphytic algae (Scheffer and Nes 2007).

In addition to seasonal changes, periphyton showed a distinctive pattern in vertical distribution. Periphyton accumulation was maximal at 30-40 cm below the water surface, while at depths higher and lower than this, its biomass and chlorophyll content declined significantly as previously been demonstrated in other lakes (Hansson 1992; Sand-Jensen and Borum 1991). This vertical distribution of epiphytic algae strongly influenced and changed the light attenuation. A good, although not perfect, correlation with the depth distribution of pelagic algal production measured in Lake Balaton was previously observed (Pálffy and Vörös 2003). The depth of maximum biomass and chlorophyll content of periphyton did not match, likely due to the fact that periphyton contained not only epiphytic algae but also resuspended organic and inorganic materials, precipitated on the surface of the plastic strips.

Potamogeton perfoliatus

As a result of increased epiphyte light quenching (especially in spring), photosynthetically available irradiance reaching the adaxial side of leaves decreased, significantly affecting the production of macrophytes. Correlation between periphyton biomass and light attenuation was high and this consequently resulted in specific seasonal and vertical patterns of *P. perfoliatus* production. Epiphytes compete for light with macrophytes and, consequently, limiting production and growth of the plant substrate (Asaeda et al. 2004; Jones and Sayer 2003).

The *P. perfoliatus* plants of Lake Balaton are physiologically well adapted to its turbulent waters, i.e. the compensation (I_c) and saturation (I_k) light intensities obtained in this study were lower than those previously described (Goldsborough and Kemp 1988; Harley and Findlay 1994; Madsen et al. 1991), while the maximal intensity of photosynthesis (P_{max}) and dark respiration (R_d) of *P. perfoliatus* were higher than previously published results (Goldsborough and Kemp 1988; Harley and Findlay 1994; Stanley and Naylor 1972; Titus and Stone 1982; Van et al. 1976). Nevertheless, it is remarkable that the only changes in

measured photosynthetic parameters (I_k and P_{max}) coincided with seasonal changes in epiphytic content (mid-June). Growing in the turbulent waters of Lake Balaton, the photosynthetic apparatus of pondweeds is capable of utilizing the available light efficiently. Moreover, it is able to respond to the change in the light environment, triggered by the decreased amount of periphyton.

The accumulation of periphyton on plastic strips and *P. perfoliatus* leaves displayed a high degree of similarity, although due to their morphological specificities (clasping leaf form and not exactly horizontal position), the plants gathered more periphyton than the strips. This periphyton accrual was concentrated on the adaxial part of the leaves, while the abaxial side hosted a very thin, inorganic crust.

This disproportionate accumulation of periphyton increases the relative importance of the upwelling, backscattered irradiance. Its significance was high, especially in the beginning of the vegetation period, but even later impacted the theoretical production of macrophytes.

Strips accumulated periphyton gradually, reaching maximum density on day 9, disregarding seasonality. This and analogous results (Brandt and Koch 2003) suggest the underestimation of pondweed production, since at the time of intense morphogenesis, a great number of leaves are not covered by epiphytes. On the other hand, the cease of morphogenesis, the rapid (within 9 day) accumulation of periphyton and the decrease of photosynthetic activity leads to the quick disappearance of *P. perfoliatus* in the monospecific stands of the study area.

Thus, periphyton can control morphological and physiological properties of the substrate plants and might provide an explanation as to some morphological and physiological phenomena of Lake Balaton macrophytes (Tóth and Herodek 2011; Tóth et al. 2011; Vári et al. 2010). According to our results, even within one plant, neighbouring leaves can show enormous differences in periphyton accumulation, which translates into large differences in both irradiance and spectral quality of the absorbed light. This light, absorbed by a leaf, can act only at limited distances (De Kroon et al. 2005), resulting in a set of very specific, local responses, a typical vertical leaf distribution pattern (Tóth et al. 2011; Vári et al. 2010). *P. perfoliatus* shows a non-conservative resource-use strategy for morphological traits (Tóth et al. 2011; Vári et al. 2010), allowing the plant to adapt to the actual

light environment at the leaf-level. In a vertically heterogeneous light environment influenced by planktonic and epiphytic light attenuation, it is advantageous for *P. perfoliatus* to have higher foliar variability, as this will result in a greater flexibility of responses and more effective light capture of plants.

Littoral zones of freshwater lakes represent a very heterogeneous habitat, with periphyton having a significant effect. Periphyton accumulation influences the production and consequently the growth and distribution of submerged rooted macrophytes. Periphyton affects the macrophytes mainly via light attenuation, and its importance in this regard should be somewhat reconsidered. The amount of periphyton accumulated on leaves depends on the type and size of the macrophyte leaves, thus it could also influence interspecific competition of macrophytes.

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Table 1. Accumulation of periphyton on plastic strips (final biomass and biomass saturation), transmittance through plastic strips, and epiphytic chlorophyll-a content at the end of the experimental period (10th day). Averages (\pm SD) of samples collected at all water depths are shown (n=14 for biomass, n=21 for transmittance, n=7 for chlorophyll). Seasonal differences are shown with t-test. *** - $P < 0.001$, ns - not significant.

	biomass			transmittance		chl-a ($\mu\text{g m}^{-2}$)	
	10 th day (mg cm^{-2})	saturation (day)		(%)			
22/03	6.8 \pm 2.9	8.7 \pm 0.5		3.9 \pm 2.2		402.9 \pm 224.0	
06/04	6.1 \pm 2.0	7.7 \pm 0.4		0.2 \pm 0.0		338.7 \pm 122.3	
20/04	4.8 \pm 1.1	10.3 \pm 1.3		2.1 \pm 1.1		612.2 \pm 213.3	
04/05	9.7 \pm 1.6	9.1 \pm 0.7		0.3 \pm 0.3		656.2 \pm 191.0	
18/05	7.6 \pm 1.6	10.4 \pm 1.2		1.0 \pm 0.8		775.7 \pm 176.1	
01/06	5.3 \pm 1.0	10.0 \pm 0.6		0.9 \pm 0.7		336.3 \pm 53.3	
15/06	2.4 \pm 0.8	10.6 \pm 1.6		18.8 \pm 10.5		302.6 \pm 101.7	
05/07	2.6 \pm 0.6	5.8 \pm 0.5		14.3 \pm 5.5		155.1 \pm 69.4	
20/07	2.3 \pm 0.3	9.3 \pm 0.2		1.1 \pm 0.3		159.9 \pm 41.6	
03/08	2.2 \pm 0.4	7.8 \pm 1.0		17.8 \pm 4.5		45.1 \pm 12.4	
17/08	2.6 \pm 0.4	8.8 \pm 1.1		7.3 \pm 3.3		99.2 \pm 26.6	
31/08	1.0 \pm 0.2	7.0 \pm 1.2		22.4 \pm 11.6		87.5 \pm 34.1	
14/09	2.3 \pm 0.3	9.9 \pm 1.3		4.0 \pm 1.5		271.4 \pm 24.4	
28/09	1.2 \pm 0.2	7.5 \pm 0.6		13.9 \pm 3.8		154.3 \pm 45.6	
t-test	7.1 ^{***}	1.6 ^{ns}		4.1 ^{***}		5.5 ^{***}	

Fig. 1. Schematic drawing of the experimental setup.

Fig. 2. Depth distribution and isopleths of periphyton biomass (**a** and **b** - mg cm^{-2}), transmittance (**c** and **d** - %) and epiphytic chlorophyll-a content (**e** and **f** - $\mu\text{g chl m}^{-2}$). Each symbol in the depth distribution graphs (**a**, **c**, **e**) is the average ($\pm\text{SE}$) of 2010 data of the given parameter collected at the specified water depth. For transmittance $n=42$, for periphyton biomass $n=28$, for epiphytic chlorophyll-a content $n=14$. Isopleths (**b**, **d**, **f**) show each parameters at the end of each 10 day experiment.

Fig. 3. Principal component scatter-diagram of periphyton biomass (biomass), transmittance (T%) and epiphytic chlorophyll-a content (chl-a). Each point shows its sampling date. Convex polygons group the spring and summer-autumn samples.

Fig. 4. Epiphytic chlorophyll-a content ($\mu\text{g m}^{-2}$) (green bars) and phytoplankton chl-a content ($\mu\text{g l}^{-1}$) (blue line) of the surrounding waters (from Présing 2011). All bars are the average ($\pm\text{SD}$) of samples collected at all water depths ($n=7$). The line is a spline polynomial fitted to biweekly measured data ($n=3$).

Fig. 5. Depth distribution of dry periphyton weight (mg cm^{-2}) within the water column on the natural (*Potamogeton perfoliatus* leaves – green symbols) and artificial (plastic strips– red symbol) surfaces measured on 2010/07/20. Red symbols represent the average ($\pm\text{SD}$) of 3 samples, while green symbols are the average ($\pm\text{SD}$) of 4 samples collected at each water depth. The inlay graph (blue symbols) presents the correlation between periphyton biomass from plastic strips and *Potamogeton* leaves ($R=0.94$, ANOVA $F=39.9$, $P=0.002$).

Fig. 6. Seasonal and vertical change of backscattered (upward) irradiance as a percentage of the periphyton absorbed downward irradiance in the eastern basin of Lake Balaton.

Fig. 7. Seasonal change in saturation photosynthesis (P_{max} - $\text{mg O}_2 \text{g}^{-1} \text{d}^{-1}$, green bars, left axis), dark respiration (R_d - $\text{mg O}_2 \text{g}^{-1} \text{d}^{-1}$, red bars, left axis), compensation irradiance (I_c - $\mu\text{mol m}^{-2} \text{s}^{-1}$, blue symbols and line, right axis) and saturation irradiance (I_k - $\mu\text{mol m}^{-2} \text{s}^{-1}$, red symbols and line, right axis) of *Potamogeton perfoliatus* in the eastern basin of Lake Balaton in 2010. Each symbol represents the average ($\pm\text{SE}$) ($n=9$).

Fig. 8. Change of production ($\text{mg O}_2 \text{g}^{-1} \text{d}^{-1}$) of *Potamogeton perfoliatus* in the eastern basin of Lake Balaton in 2010 along the vegetation period at different depths calculated on the basis of only downwelling irradiance (a), on the biofilm quenched downwelling irradiance (b) and sum of the biofilm quenched downwelling and upwelling irradiances (c).

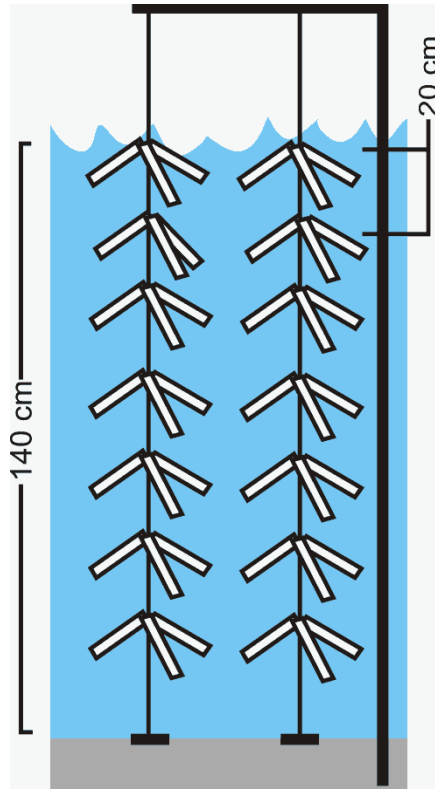


Fig. 1.

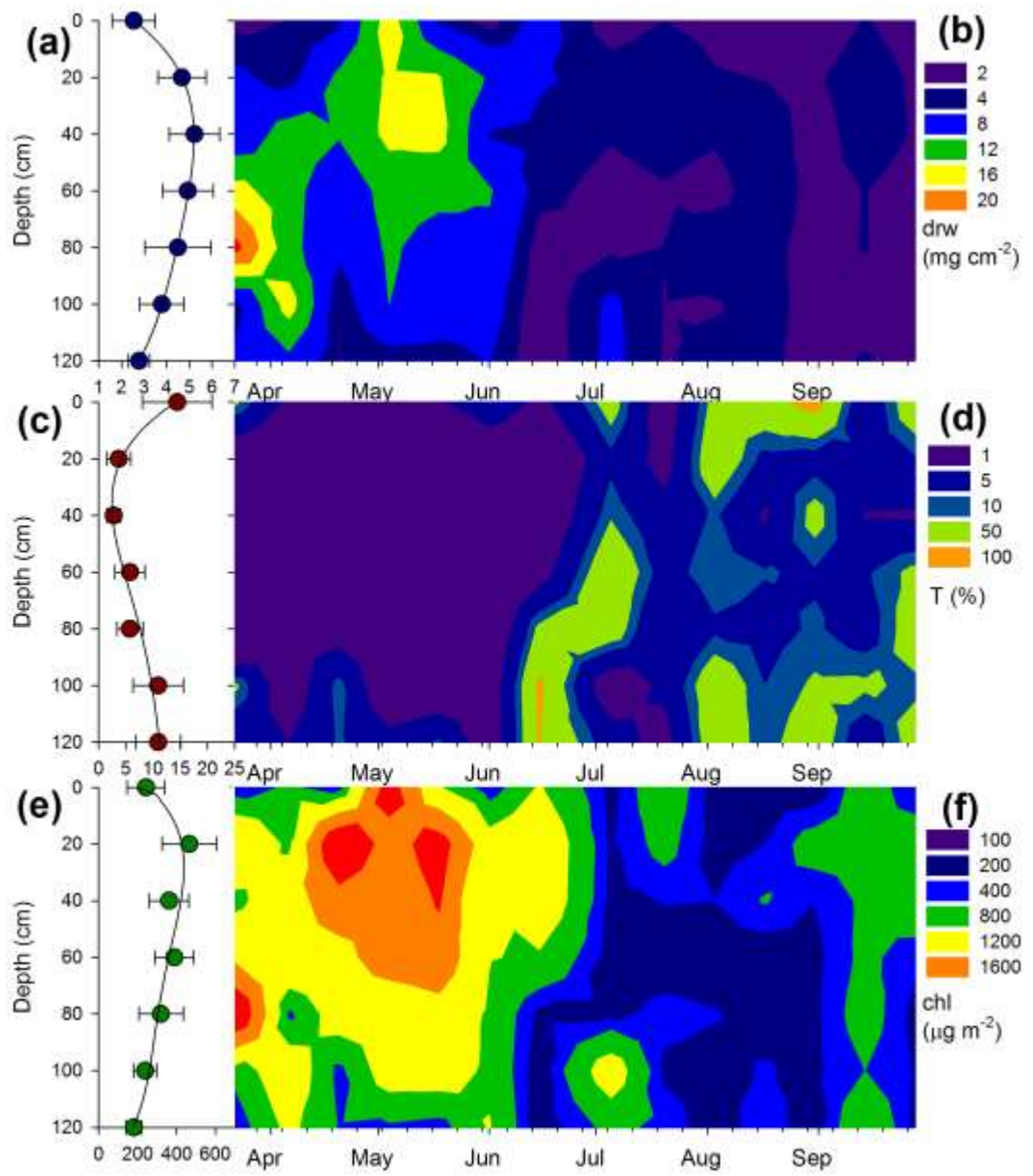


Fig. 2

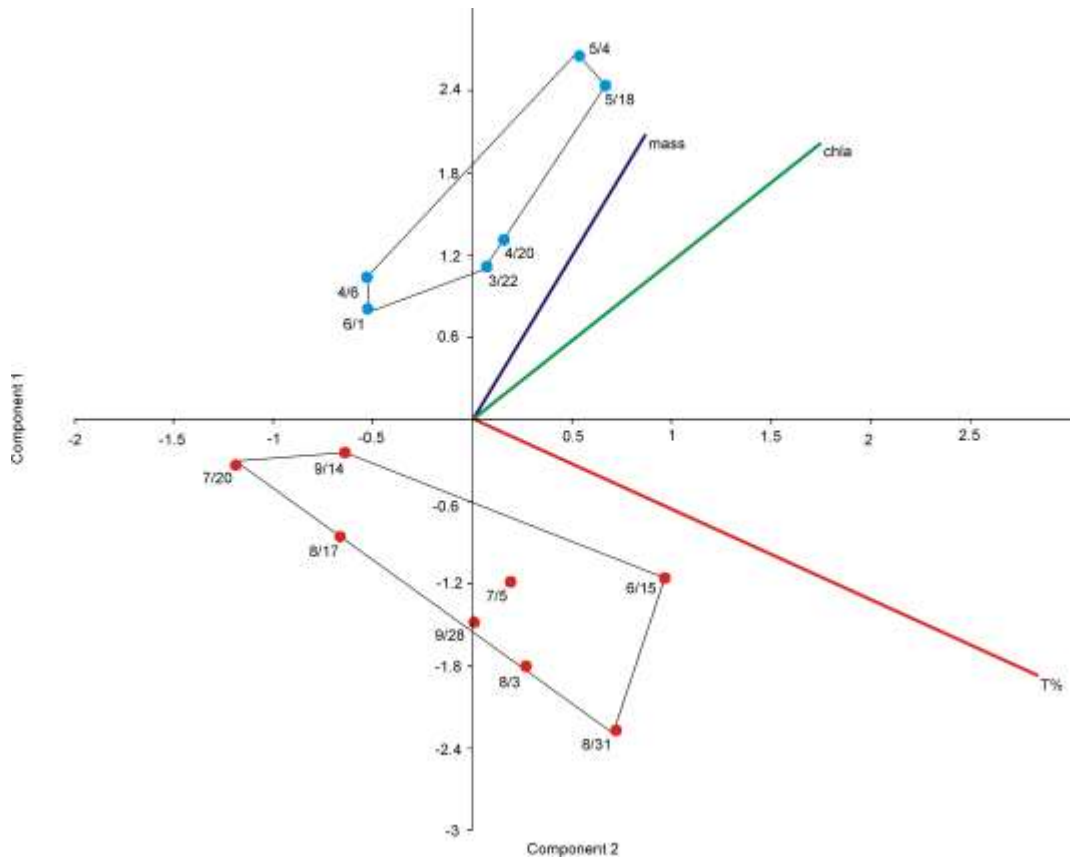


Fig. 3.

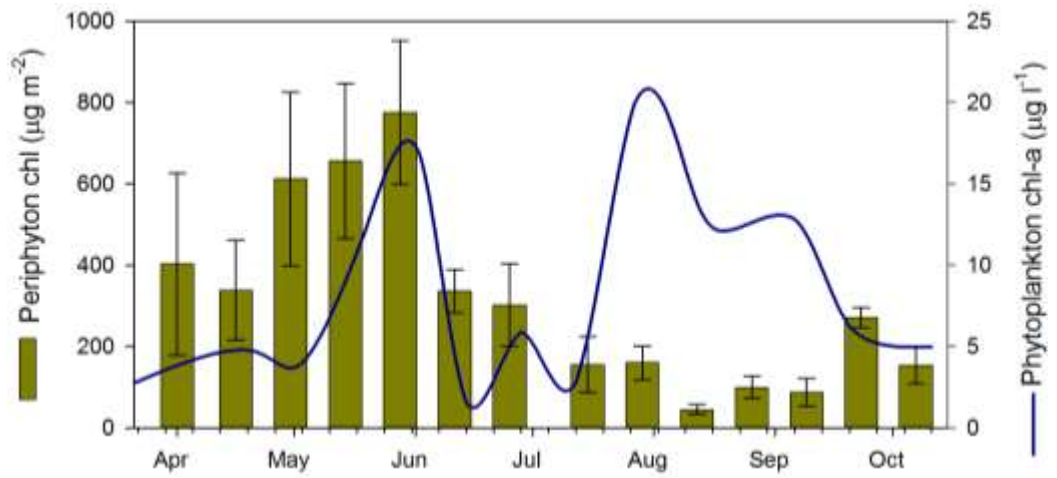


Fig. 4.

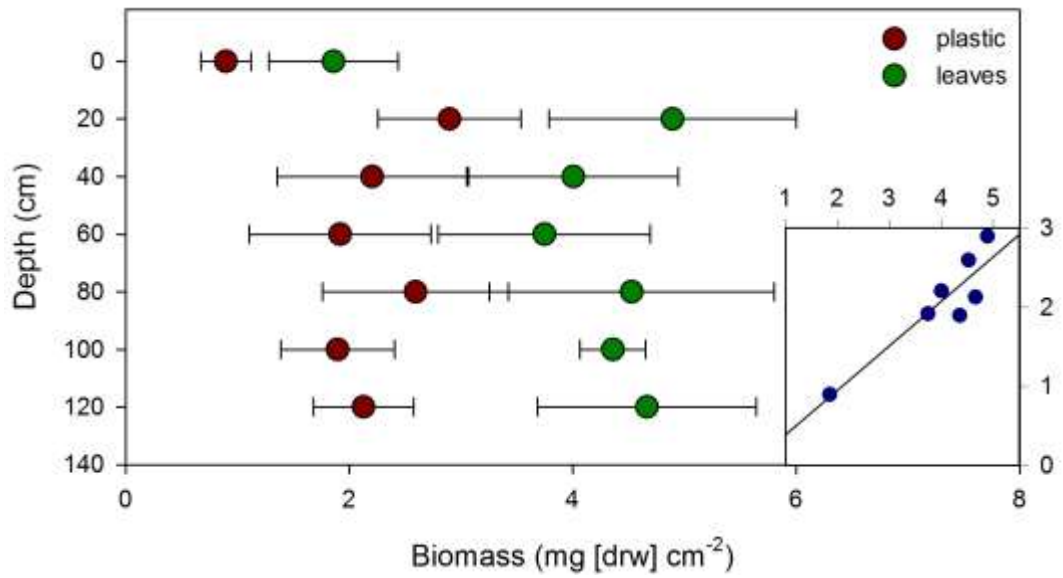


Fig. 5.

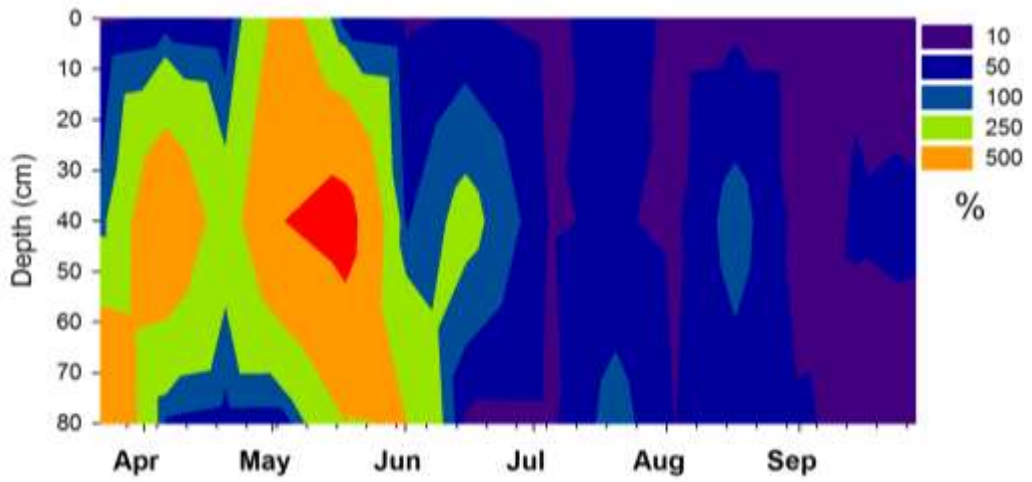


Fig. 6.

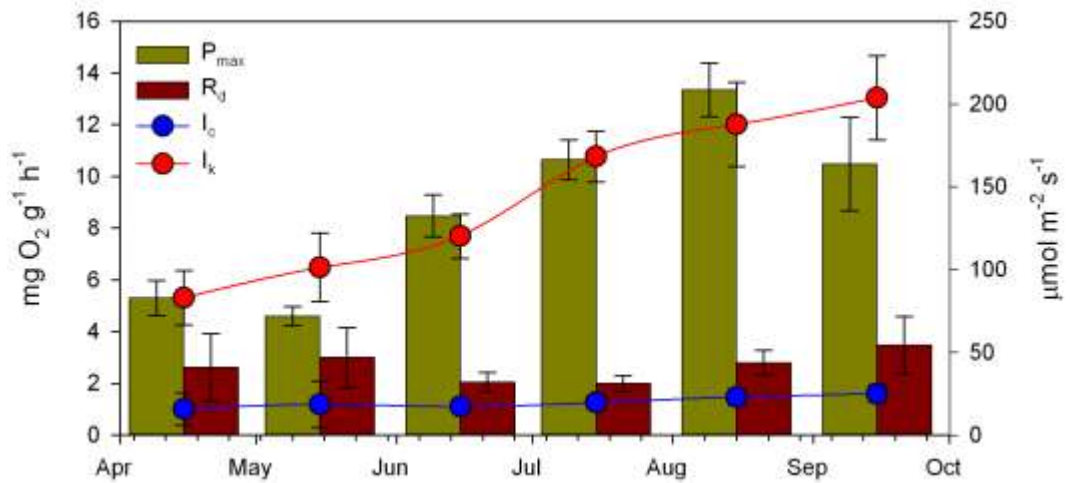


Fig. 7.

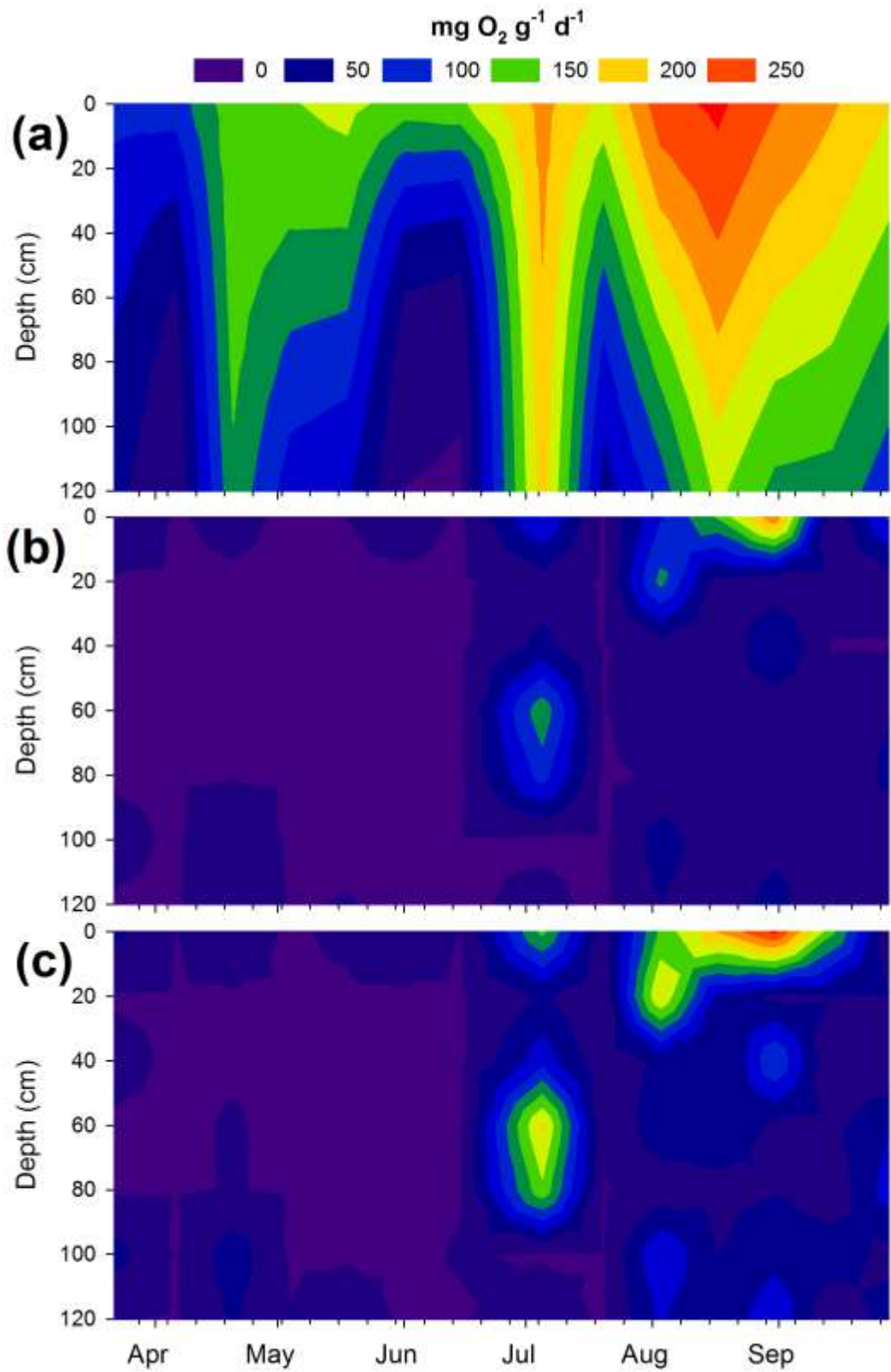


Fig. 8.