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Morphological and photosynthetic acclimation of *Potamogeton perfoliatus* to different environments in Lake Balaton

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Key words: morphology, photosynthesis, *Potamogeton perfoliatus*, Lake Balaton, acclimation, light

Abstract

Comparative significance and synchronicity of morphological and photosynthetic adjustments of *Potamogeton perfoliatus* to shore-specific environments were examined on plants growing at the maximum depth of colonisation of the northern and southern shores of Lake Balaton. The shore-specific environments did not affect photophysiological parameters: the photosynthesis of plants on both shores was high, coupled with low respiration and compensation irradiances. In contrast, morphological and habitual differences between the shores were significant: plants of the shady, northern shore had lighter, but larger leaves, and longer internodes concentrated in the apex of the plants. Thus, photophysiological variability of *Potamogeton* does not follow its morphological differentiation.

Introduction

Primary production of submerged macrophytes is a function of the depth-specific photosynthetic response of each leaf to irradiance within the water column and of the vertical distribution of photosynthetically effective canopy area. Thus, production is affected by both physiological and morphological variability and their responses to environmental factors. Variability of morphological and photo-physiological traits is an important mechanism for surviving in the aquatic environment (Bowes and Salvucci 1989, Santamaría and van Vierssen 1997, Santamaría 2002, Wells and Pigliucci 2000). Although the mechanisms of these actions are well understood, little is known about their interconnection and hierarchy. Metabolic and morphological adjustment to changes of environment tend to manifest in unison (Gutschick 1999), however it would be interesting to learn which of these processes is more reactive. This work aims to clarify whether photobiological acclimation of clasping-leaf pondweeds (*Potamogeton perfoliatus* L., Potamogetonaceae) follows the striking morphological variability of plants.

Lake Balaton is a large (596 km^2), relatively shallow (average depth ~3.5 m) freshwater lake in the centre of the Pannonian Basin. The prevailing regional (northern) wind determines the content of the lake bottom: wind generated north-south orientated underwater currents sediment the fast precipitating sand on the southern shore, while the manganese-rich calcite of high organic content drifts along towards the northern shore. This results in the different light climates of the northern and southern shores (Tyler et al. 2006). Despite this significant difference, the *P. perfoliatus* of the northern shore can be found at greater depths (maximum depth of colonisation ~2.3 m), while the more transparent

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waters of the southern shore are colonised up to a depth of ca. 1.3 meters. This optical heterogeneity and the wave impacts on the southern shore of Lake Balaton consequently could influence the metabolic and morphological properties of *P. perfoliatus*.

Light is crucial for submerged rooted macrophytes (Abernethy et al. 1996, Asaeda et al. 2004, Goldsborough and Kemp 1988, Sabbatini and Murphy 1996). *P. perfoliatus* plants live under very different irradiances, however they are categorised as shade-tolerant plants (Bowes and Salvucci 1989). Suboptimal irradiance triggers extensive morphological (shade-tolerance) (Barko et al. 1982, Pilon and Santamaría 2001, Asaeda et al. 2004) and architectural (shade-avoidance) (Goldsborough and Kemp 1988, Asaeda et al. 2004, Wolfer et al. 2006) modifications with the aim of boosting the capture of radiation. Mechanical disturbance also can significantly affect the distribution of macrophytes, mostly affecting their morphological and habitual properties (Eriksson et al. 2004).

On the other hand, photosynthesis of submerged aquatic plants is equally variable (Asaeda et al. 2004, Goldsborough and Kemp 1988, Madsen and Adams 1989, Pilon and Santamaría 2001, Tóth and Herodek 2008). Submerged macrophytes typically show low gas exchange rates (both photosynthesis and dark respiration) and low compensation irradiances, but at saturating (optimal) light intensities can produce significantly higher photosynthetic and respiratory rates (Bowes and Salvucci 1989, Duarte 1991, Rae et al. 2001).

Thus it might be assumed, that photomorphogenic variability of *P. perfoliatus* is accompanied by photophysiological changes. In this work we hypothesised that plastic responses of *P. perfoliatus* exposed to the different environmental conditions of the northern and southern shores are present simultaneously on both morphological and photosynthetic levels. We tested this hypothesis in populations of *P. perfoliatus* growing at the maximal depth of colonisation in the littoral zones of the less illuminated northern and well-lit southern shores of Lake Balaton. Evaluation was performed by comparing leaf and shoot morphology of plants of the northern and southern shores of Lake Balaton as distributed within the water column, while testing their photosynthetic capacity and by analyzing the effect of different environments on the development of morphological and photosynthetic traits of *P. perfoliatus*.

MATERIALS AND METHODS

Sampling sites and plant material

Sampling sites were selected in the easternmost basin of Lake Balaton (Fig. 1). These points were chosen because of the optical difference between the shores, the same trophic state and presence of clasping-leaf pondweed (*Potamogeton perfoliatus* L.).

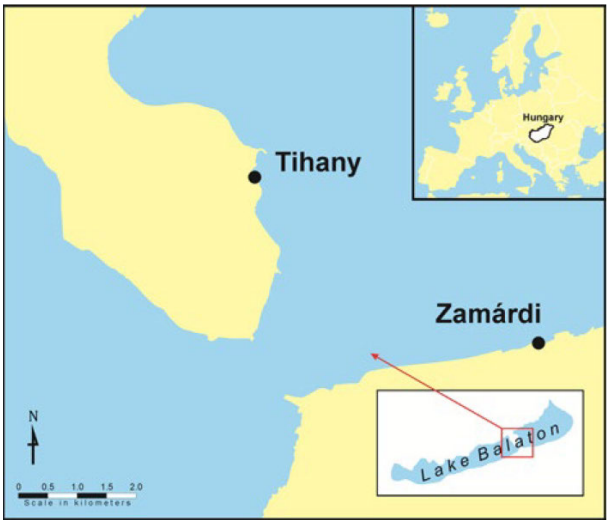


Fig. 1. Map of Lake Balaton and sampling sites on the northern (Tihany) and southern (Zamárdi) shores.

The sampling point on the northern shore of Lake Balaton was at the eastern side of Tihany peninsula (N 46°54'50.04", E 17°53'37.36") with typical manganese-rich calcite of high organic content sediment and steep lake bottom (Fig. 1). At this site *P. perfoliatus* plants were situated in 1.3 – 2.1 meter deep water. The sampling point on the southern shore (N 46°53'29.06", E 17°57'49.08") was near the village Zamárdi, in front of a small, 120-180 meter wide reed bed (Fig. 1) where the pondweed plants were in 0.4 – 1.0 meter deep water. At both sites sediment was sampled at three points and analysed for total P (HNO_3-H_2O_2 digestion with ammonium-molibdenate method), total N (phenol sulphuric digestion with macro-Kjeldahl method) and total K (HNO_3-H_2O_2 digestion with atomic absorption spectrophotometer measurement) content to ensure no nutrient shortage occurred.

At the northern sampling site, water temperature and irradiance at different depths were measured throughout the year with pendant temperature and light sensors (Onset Computer Corporation, US). On the southern shore irradiances at several depths and

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temperature were measured occasionally during the sampling of plants. From the slope of the linear regression of averaged irradiances collected by depth and related to the depth of measurements the light attenuation coefficient (K_d, m^{-1}) of the whole water column with plants was calculated.

Between the 1st and 16th of August 2007 *P. perfoliatus* on the northern and southern shores were collected on eight occasions at each site. Sampling took place over big areas (ca. 300 m^2) from the maximum depth of colonisation, i.e. at a depth of 1.9 – 2.1 m on the northern and 1 meter on the southern shore. Intact, healthy looking *Potamogeton* plants (25 – 30 plants per site) with roots were collected and transported within minutes to the laboratory in a darkened cooling box filled with lake water.

Morphology

Plants for morphology were randomly chosen and separated (3-4 plants each sampling event, with a total of 16 plants each site). The biometric measurements were performed either on the day of sampling or the next day. Pondweeds were kept in a refrigerator at 4°C until biometric measurements could be performed. Whole *P. perfoliatus* plants were cleaned of periphytic algae, resuspended sediment and epiphytic organisms with a soft brush or by hand and thoroughly washed with lake water. After shoot length determination (from the 1st internode to the tip of the upper leaf), leaves were removed one-by-one, scanned (Canoscan LiDE60, Canon, Japan), dried at 60°C for 10 days (Heraeus T6, Heraeus, USA), and then dry weight was determined (Ohaus Explorer, Ohaus Corp., USA). To calculate the position of each leaf within the water column, the length of each internode was measured with a millimetre precision ruler. The digitized leaves were processed using ImageJ (version 1.36, http://rsb.info.nih.gov/ij/) to determine length, width and area of each leaf.

Photosynthesis measurements

Six healthy looking *P. perfoliatus* were chosen for every single photosynthetic measurement. From the basal, middle and apical part of each plant, three fully matured, intact leaves were collected and transferred to 300 ml Karlsruhe vials (WTW, Germany) filled with filtered (pore size 0.45 μm) lake water. All 18 Karlsruhe vials (three vials for each irradiance) were placed into an incubation tank specially designed for photosynthesis measurements (Tóth and Herodek 2009). Leaves were preincubated for 30 minutes in darkness, while the temperature of the cooling-heating bath (Neslab RTE-17, Thermo Electron, USA) was set to the actual water temperature at the sampling sites (Fig. 2). Mixing was provided by stirring bars and specially made magnetic stirrers (rotation speed - 30 rpm) placed under the incubation tank (Tóth and Herodek 2009). Oxygen

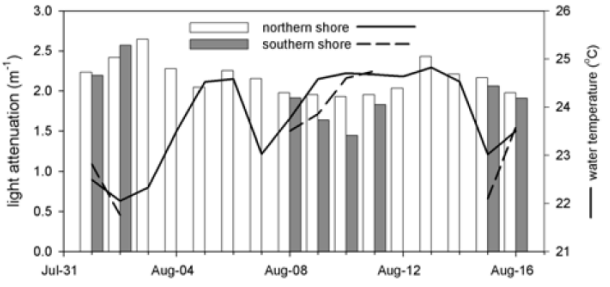


Fig. 2. Vertical light attenuation coefficient (K_d – m^{-1}) and water temperature (°C) at the studied sites during the sampling events.

production by photosynthesis and consumption by dark respiration was recorded with an oxygen electrode (TriOxmatic 300, WTW, Germany) connected to a data logger (Oxi 539 microprocessor precision oxygen meter, WTW, Germany) at 6 light intensities (from 18 to 780 μmol m^{-2} s^{-1}) or with the light sources switched off (Tóth and Herodek 2009). The pH and DIC of the incubation media was monitored at the beginning and the end of each measurement and the changes were less than 1%. This procedure was repeated seventeen times between the 1st and 16th of August at different sites.

Calculations and statistical analysis

Each photosynthesis data set (18 light and 18 dark points) was fitted with an exponential saturation model as per Platt (Platt et al. 1980):

$$P = P_s\left(1 - e^{-\frac{\alpha I}{P_s}}\right)e^{-\frac{\beta I}{P_s}} \quad (1)$$

where $\boldsymbol{P}$ – (mg O_2 g [drw] $^{-1}$ h^{-1}) is the photosynthetic activity at the $\boldsymbol{I}$ irradiance (μmol m^{-2} s^{-1}), $\boldsymbol{P_s}$ – is the actual light saturated photosynthetic activity, $\boldsymbol{\alpha}$ is the photosynthetic, $\boldsymbol{\beta}$ is the inhibition coefficient. From the equation 1 the following parameters were calculated:

P_{max} – maximal photosynthetic rate

$$P_{max} = P_s\left(\frac{\alpha}{\alpha+\beta}\right)\left(\frac{\beta}{\alpha+\beta}\right)^{\frac{\beta}{\alpha}} \quad (2)$$

I_k – saturation irradiance

$$I_k = \frac{P_{max}}{\alpha} \quad (3)$$

I_c – compensation irradiance

$$I_c = \frac{P_s\left(-ln\left[1-\frac{R_d}{P_s}\right]\right)}{\alpha+\beta} \quad (4)$$

where $\mathbf{R_d}$ is dark respiration [mg O_2 g[drw]$^{-1}$ h^{-1}]

I_b – irradiance at which the inhibition of photosynthesis starts

$$I_b = \frac{P_s}{\beta} \quad (5)$$

For curve fitting (least-squares technique) Sigma Plot v 8.0 (Systat Software Inc., USA) was used. For all curves fitted ANOVA was performed.

Phenotypic plasticity index of morphological parameters was calculated for each plant separately by comparing the maximum amplitude and minimum amplitude relative to the maximum amplitude ((max-min)/max) of the studied parameter. Phenotypic plasticity index of the photosynthesis results was calculated on the basis of results measured at one site.

The comparison of morphological and photosynthetic parameters from the northern and the southern shore was made by t-test. Assumptions of normality and homoscedascity were tested and, when necessary, data were transformed to attain a normal distribution. A General Linear Model (GLM) test on morphological parameters was performed with shorelines (northern and southern) as categorical, depth as continuous and plants as random variables. For statistical analysis RExcel v.3.0.17 (http://rcom.univie.ac.at/) was used (Baier and Neuwirth 2007).

RESULTS

Distinct geomorphologic (steep vs. shallow) and sedimentologic (calcite vs. sand) differences between the northern and southern shores of the lake resulted in higher light attenuation coefficients on the northern shore (2.2 ±0.2 m^{-1} vs. 1.9 ±0.3 m^{-1}) (Fig. 2). Consequently, on the northern shore at the studied depth (ca 2.0 m) the majority of leaves (56%, i.e. the lower 29 nodes) of *P. perfoliatus* received on average less light (<265 μmol m^{-2} s^{-1}) than the basal leaves of plants on southern shore (~1 m deep).

The nutrient content of the sediment at the studied sites was very similar. Both total nitrogen (3.8 ±2.0 vs. 2.0 ±0.1 g kg^{-1}) and total K (3.7 ±0.3 vs 2.7 ±0.3 g kg^{-1}) were slightly higher on the northern shore as compared to the southern shore, but neither N or K, nor the total P content (206.5 ±33.0 vs 250.1 ±25.5) was significantly different from shore to shore.

Photosynthetic parameters

The light response curves of photosynthesis were typical, characterizing the underlying photophysiological processes, i.e. the efficiency of light utilisation and CO_2 uptake of *P. perfoliatus* (Fig. 3). Each set of measured data of photosynthesis and dark respiration was fitted with a saturation curve (Platt et al. 1980) (see Materials and Methods), ANOVA on fitted curve was performed (all $P<0.005$ and $R^2>0.92$) and hereafter calculated parameters are presented.

Theoretical maximal intensity of photosynthesis (P_{max}) of *P. perfoliatus* on the northern shore changed between 26 and 48 mg O_2 g[drw]$^{-1}$ h^{-1}, while on the southern shore these parameters were between 16 and 78 mg O_2 g[drw]$^{-1}$ h^{-1} (Table 1). Dark respiration (R_d) of pondweeds on both shores did not differ significantly, so the intensity of respiration stayed nearly constant and varied between 4.1 ±0.9 and 4.5 ±2.9 mg O_2 g[drw]$^{-1}$ h^{-1}) on the northern and southern shores, respectively (Table 1). The data of theoretical maximal intensity of photosynthesis and the data of theoretical dark respiration were identical to the actually measured photosynthesis at saturation irradiances (780 μmol m^{-2} s^{-1}) and the data of measured dark respiration (t-test, t=0.24, P=0.81 and t=0.39, P=0.70). The ratio of dark respiration to P_{max} was low and stayed around 13–14%.

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Table 1

Photosynthetic parameters (mean ±standard deviation) of *Potamogeton perfoliatus* from the northern and southern shores of Lake Balaton and t-test results.

	mean ±SD		t-test
	northern	southern	t^P
P_{max} (mg O_2 g[drw]$^{-1}$ h^{-1})	41.5 ±14.8	39.7 ±20.8	-0.5 ^{ns}
R_d (mg O_2 g[drw]$^{-1}$ h^{-1})	4.1 ±0.9	4.5 ±2.9	-0.6 ^{ns}
R_d/P_{max} (%)	13.4 ±6.6	15.2 ±9.8	-0.5 ^{ns}
I_c (µmol m^{-2} s^{-1})	7.7 ±3.4	9.3 ±4.9	-0.2 ^{ns}
I_k (µmol m^{-2} s^{-1})	161 ±59	108 ±43	**2.2***
I_b (µmol m^{-2} s^{-1})	1057 ±471	8147 ±1570	**-4.2*****
α (mg O_2 g[drw]$^{-1}$ h^{-1}/µmol m^{-2} s^{-1})	0.24 ±0.04	0.39 ±0.10	**-2.2***

P_{max} – maximum photosynthetic rate, R_d – dark respiration, I_c – compensation irradiance, I_k – theoretical saturation irradiance, I_b – irradiance of photoinhibition, α – photosynthetic light use efficiency, $\alpha = P_{max}/I_k$.

Significance: ns – P ≥ 0.05, * – P < 0.05, ** – P < 0.01, *** – P < 0.001
For all tests n=17.

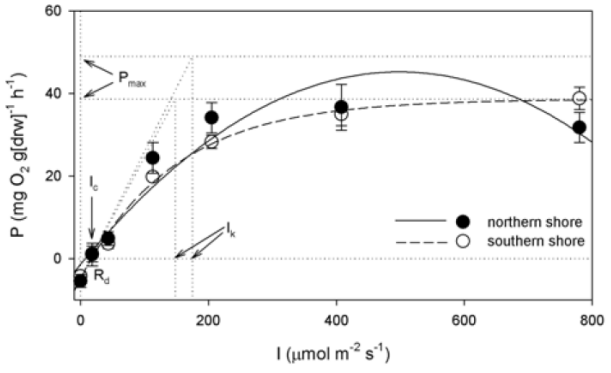


Fig. 3. Response of photosynthesis of *Potamogeton perfoliatus* to different light intensities. Each symbol is average ±SD (n=3). The represented line is a fitted exponential saturation equation (Platt et al. 1980). All shown $R^2 > 0.96$, the significances of the Analysis of Variance are $P < 0.003$. The shown parameters are: P_{max} – maximal photosynthetic rate (mg O_2 g[drw]$^{-1}$ h^{-1}), R_d – dark respiration rate (mg O_2 g[drw]$^{-1}$ h^{-1}), and I_k and I_c are saturation and compensation irradiances (µmol m^{-2} s^{-1}).

Compensation irradiance (I_c) on the northern shore didn't differed statistically from the data measured on plants from the southern shore (7.7 ±3.4 and 9.3 ±4.9 µmol m^{-2} s^{-1}, respectively, Table 1), while theoretical saturation irradiance (I_k) of *P. perfoliatus* on the northern shoreline was significantly higher, than the I_k of plants on the southern shoreline (161 ±59 vs. 108 ±43 µmol m^{-2} s^{-1}, respectively, Table 1). The irradiance at which inhibition of photosynthesis started (I_b) also significantly differed between the shores, as the northern shore plants showed inhibition of their photosynthesis at an irradiance well under the maximal detectable light intensity of the sun (1057 ±471 µmol m^{-2} s^{-1}). On the other hand, plants of the southern shore showed no light inhibition (average I_b was much higher than 2100 µmol m^{-2} s^{-1}, Table 1). The light capture efficiency (α) of plants from the northern shore was lower than of plants on the southern shore (Table 1).

Morphological parameters

Leaves of *P. perfoliatus* plants from the northern shore reached their maximum length (3.3 ±0.7 cm, Table 2) within 8 internodes (~45 cm, Fig. 4A) from the apex of the plants, while on the southern shore the longest leaves (2.6 ±0.6 cm, Table 2) were found at the basal part of the plants (39th node, ~78 cm from apex, Fig. 4A). The difference between the widths of leaves in the studied plants was less significant (Table 2), though leaves on plants from the northern shore were slightly (~5%) narrower than on the southern shore (2.2 ±0.5 versus 2.3 ±0.4 cm, respectively). The depth distribution of leaf width had the same spatial pattern as the distribution of leaf length on plants from both the northern and southern shorelines (Fig. 4B).

Leaf area of plants from the northern shoreline was significantly (ca. 15%) higher (Fig. 5A and Table 2). The biggest leaves were situated on the 6th and 7th node from the sediment on plants of the northern and southern shores, respectively. On the northern shore the majority (ca. 60%) of leaves had an area close to maximum (5.7 ±2.1 cm^2, Table 2) and this size was reached within 30 cm of the shoot tip (Fig. 5A). On the southern shore 15% of leaves of *P. perfoliatus* were close to the maximum area (4.8 ±1.6 cm^2, Table 2) and this size range concentrated at the basal 15% of the plant (Fig. 5A).

Leaves of *Potamogeton* plants from the southern shore were on average 25% heavier than the leaves from the northern shore (Fig. 5B, Table 2). Specific leaf weights (SLW, i.e. leaf dry weight per leaf area) of pondweed plants collected from the southern shore were significantly (36%) higher than that of plants from the northern shore (Fig. 6A, Table 2). The SLW of leaves from northern plants changed between 1.1 and 2.7 mg cm^{-2} with no significant deviations (1.9 mg cm^{-2} in the upper and 2.4 mg cm^{-2} in the lower parts of the canopy), while on the southern shore the data varied between 1.4 and 4.6 mg cm^{-2}, showing a constant increase with depth from 1.6 to 4.3 mg cm^{-2} (Fig. 6A).

Internodes on the northern shore of Lake Balaton were significantly longer than on the southern shore (Fig. 6B, Table 2). The most striking difference was

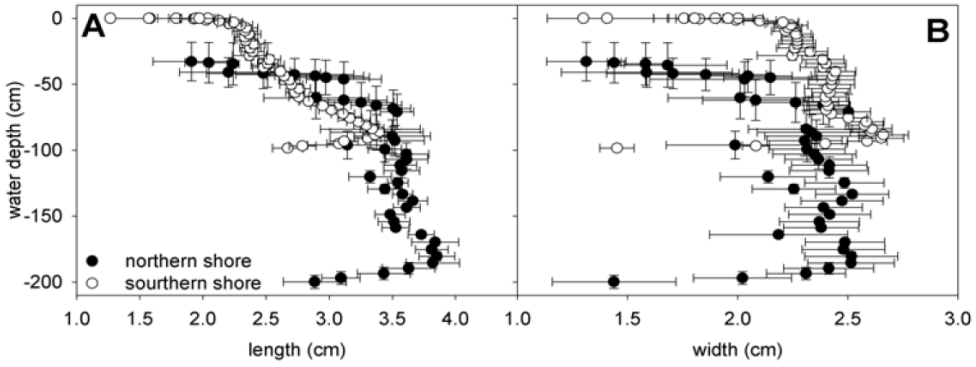


Fig. 4. Length (A) and width (B) of *Potamogeton perfoliatus* leaves at different depth on the northern (black circles) and southern (white circles) shores of Lake Balaton. Each symbol is average ±SD (n = 1−16).

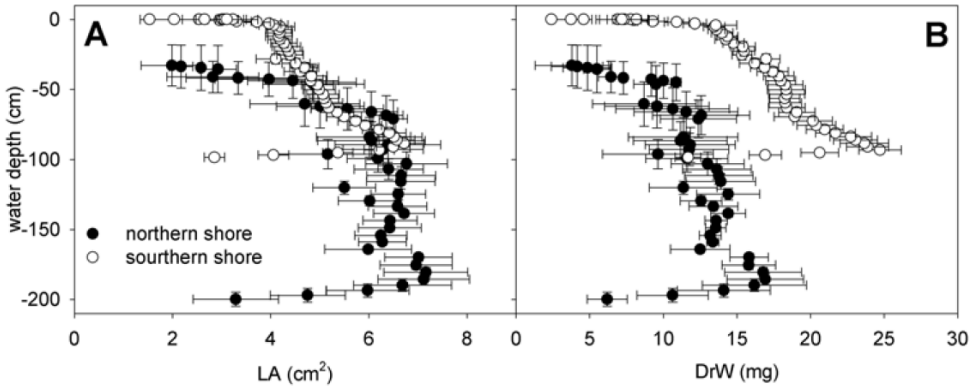


Fig. 5. Area (A) and dry weight (B) of *Potamogeton perfoliatus* leaves at different depths on the northern (black circles) and southern (white circles) shores of Lake Balaton. Each symbol is average ±SD (n=1−16).

Table 2

Morphological parameters (average ±standard deviation) of *Potamogeton perfoliatus* from the northern and southern shores of Lake Balaton and t-test results between the shores (t^P). Results (F^P) of the General Linear Model (GLM) test on the morphological parameters. In the model the morphological parameters were the dependent variables, shorelines (northern and southern) were as categorical, depth as parametric and plants as random independent variables. Depth correlation (R^P) of morphological parameters on the northern and southern shores.

	leaf length (cm)	leaf width (cm)	length to width ratio	leaf area (cm^2)	total leaf area (cm^2)	leaf dry weight (mg)	SLW (mg cm^{-2})	internode length (cm)
northern	3.3 ±0.7	2.2 ±0.5	1.5 ±0.3	5.7 ±2.0	190.3 ±52.6	12.3 ±5.4	2.1 ±0.6	3.9 ±1.8
southern	2.6 ±0.6	2.3 ±0.4	1.1 ±0.2	4.8 ±1.6	177.2 ±33.1	16.5 ±6.2	3.3 ±0.6	2.5 ±1.2
	t-test (t^P)							
	14.2 ***	**-2.9** **	**-24.8** ***	**5.9** ***	0.7 ns	**-8.6** ***	**-26.9** ***	**11.1** ***
variables	GLM test (F^P)							
depth	**631.7** ***	**91.5** ***	**273.4** ***	**317.4** ***	–	**497.9** ***	**132.9** ***	**19.2** ***
shore	5.9 ns	0.9 ns	**8.3** *	0.0 ns	–	**22.9** ***	**63.9** ***	5.2 ns
plant	1.8 ns	1.2 ns	0.6 ns	1.1 ns	–	3.3 ns	**8.1** *	0.2 ns
depth × shore	**102.5** ***	3.6 ns	**20.9** ***	**34.1** ***	–	**16.9** ***	**7.8** *	**23.8** ***
	correlation with depth (R^P)							
northern	**-0.35** ***	**-0.18** *	-0.07 ns	**-0.25** **	–	**-0.38** ***	**-0.19** *	**-0.39** ***
southern	**-0.69** ***	**-0.27** ***	**-0.68** ***	**-0.53** ***	–	**-0.59** ***	**-0.22** ***	-0.01 ns

Significance: ns – P ≥ 0.05, * – P < 0.05, ** – P < 0.01, *** – P < 0.001. For the GLM test n is at least 831, for t-test and correlation n is at least 250.

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in the pattern of distribution of internode length within the water column (Fig. 6B). With depth the internodes increased their length, but while the length of internodes from southern *P. perfoliatus* reached near maximum values (~2.5 cm) within mere centimetres from the apex of plants and stayed nearly the same size until the basal 15% of the plant (Table 2, Fig. 6B), the internode length of pondweeds from the northern shore increased gradually from 0.6 cm in the apex to 5.5 cm close to the sediment (Table 2, Fig. 6B).

Depth was appointed as the main cause of variation of morphological data by the general linear model (Table 2). The GLM test showed that depth (and consequently light attenuation) is more likely to explain the shape of the variance of all morphological data (Table 2), while an undisclosed shore-specific variable, which could not be specified in this study, was attributed as an influential factor only for length to width ratio, leaf dry weight and specific leaf weight (Table 2). A single plant-specific variable corresponded to the changes of the specific leaf weight (Table 2). The variance of leaf length and leaf dry weight was the most powerful, while the internode length was the least affected parameter (Table 2). Nearly all the morphological data had significant depth correlation (Table 2).

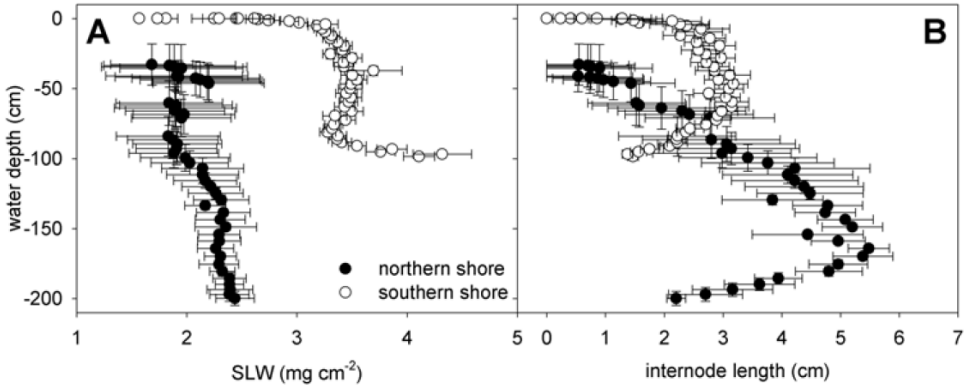


Fig. 6. Specific leaf weight (A) and internode length (B) of *Potamogeton perfoliatus* plants at different depths on the northern (black circles) and southern (white circles) shores of Lake Balaton. Each symbol is average ±SD (n=1–16).

DISCUSSION

Maximal photosynthetic capacity (P_{max}) of *P. perfoliatus* on both shores was higher than data of previous studies (Caffrey and Kemp 1991, Harley and Findlay 1994), but it agreed with our earlier results (Tóth and Herodek 2008). It was paired with low dark respiration, low compensation and saturation irradiances, thereby showing physiological signs of shade tolerance. The intensity of dark respiration and compensation irradiance were lower than the previously published results (Goldsborough and Kemp 1988, Harley and Findlay 1994, Madsen et al. 1991). However, there was no shore specificity in major photosynthetic parameters (Table 1).

Contrary to photosynthesis, the morphology of *P. perfoliatus* showed shore-specific acclimation. *Potamogeton* from the southern shore had significantly smaller leaves (area by ~17%, Table 2) than their northern counterparts, while leaves of plants from the northern shore were significantly lighter (by 35%, Table 2), resulting in a lower specific leaf weight and supporting the idea of morphological shade acclimation described previously (Larcher 2003, Markager and Sand-Jensen 1994, Vári et al. 2010). Increase of light intercepting surface area in low-light regions enhances the fitness of shade-adapted plants, but successful shade-avoidance can also help with survival. *P. perfoliatus* showed a strong, habitual, light-related shade-avoidance trait (Fig. 6B, Table 2), since in the less illuminated waters (both in general from the northern shore or from deeper waters) the length of the internodes significantly increased (Fig. 6B, Table 2), helping plants to focus their photosynthetic biomass into the more illuminated surface waters.

Since there was no indication of difference in major photosynthetic parameters between the northern and southern shores, we tested only morphological data with the General Linear Model (GLM), trying to identify the most influential

variable. Statistical analysis of these data showed that depth, or more significantly the depth-related attenuation of irradiance, is the variable most affecting the distribution of morphological parameters (Table 2). Depth correlation of the studied morphological parameters shows the sensitivity of each parameter both on the northern and southern shores to the gradient of light: on the northern shore the length of internodes is the most sensitive parameter while the width of leaves is the least influenced, while on the southern shore length of leaves correlates most strongly with the depth while the internode length does not show significant correlation with depth (Table 2).

There is a significant positive impact of the shore as a specific variable affecting the distribution of some morphological parameters (length to width ratio, leaf dry weight and SLW, Table 2) of *P. perfoliatus*. This weaker, shore-specific factor affecting distribution of the morphological variables is connected to the southern shore, thus wave exposure may be the factor that also plays an important role in regulating the morphology of *Potamogeton*. The affected parameters could be used as descriptors of leaf robustness (low length/width ratio, high dry weight and SLW), thus the magnitude of these parameters suggest the successful acclimation of the studied plants at the southern shore to wave impacts. Besides this, the significant correlation with the wave impacts could explain the lower depth of colonisation of *P. perfoliatus* on the well-lit southern shore as compared to the northern shore.

From our measurements we learned that the basal half (lower 84 cm) of *P. perfoliatus* plants on the northern shore were in a suboptimal light environment (below I_k), while the apical part of plants were in a supraoptimal light environment (Fig. 2 and Table 1). Macrophytes on the southern shore situated entirely in the optimal (over I_k) irradiance (Fig. 2 and Table 1). Theoretically, a plant existing in a gradient of a determinant environmental factor will disrupt its overall phenotypic integrity and show significant variability (Bassow and Bazzaz 1997, Gutschick 1999, Torres Boeger and Poulson 2003). Nevertheless, our results showed a lower within-plant phenotypic plasticity of photosynthetic parameters on the northern shore, as compared to the southern shore and no difference between the phenotypic plasticity of the morphological parameters (Table 3).

CONCLUSIONS

In summary, the photosynthetic apparatus of *P. perfoliatus* is physiologically well acclimated to the turbulent water of Lake Balaton. Moreover, the pondweed populations from both shores of the lake are primarily photophysiologically acclimated to lower irradiances. Growing in the deep, shady waters, the photosynthetic apparatus of pondweeds is capable of utilizing the available light efficiently, but reaching the more illuminated waters the pondweed is inept at adjusting its photophysiology to higher irradiances. Thus it could be assumed that our hypothesis is not supported, i.e. in the case of clasping leaf pondweeds, variability of photosynthesis does not follow the non-cryptic morphological heterogeneity of plants.

Our results also showed that morphological light acclimation of *P. perfoliatus* is more dominant and better correlated to the light environment of growth, although shore-specific factors (wave impact) have a significant influence on data distribution as well. Leaf morphological parameters and plasticity are more relevant determinants of *P. perfoliatus*'s acclimation during the transition from low to high irradiances, showing signs of both shade-tolerance (increased leaf area) and shade avoidance (increased internode length).

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