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Editor's choice

Impact of habitat environment on *Potamogeton perfoliatus* L. morphology and its within-plant variability in Lake Balaton

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Abstract – Plastic effect of environmental factors acting on an aquatic submerged plant, *Potamogeton perfoliatus* L. at the plant-level (nutrient availability) and the leaf-level (light intensity) at different sites in Lake Balaton was studied. Light-dependent morphological traits (foliar morphology and internode length) of *P. perfoliatus* were measured and analysed across the environmental gradients of the lake. The size of leaves was influenced by both trophic state and light environment: nutrient surplus increased the size of leaves by ~ 29%, whereas a more heterogeneous light environment resulted in 15% larger leaves. The light environment influenced shoot morphology (internode length) to a greater extent than nutrient surplus (38% vs. 19%). Contrary to this, within-plant morphological variability was significantly higher (41%) at the nutrient limiting sites as a result of diversification effect of the leaf-level environmental factor, light. Foliar parameters and within-plant variability showed correlation only with the total N content of the sediment. Appearance of *P. perfoliatus* is shaped by counteracting effects: within-plant differentiation, promoted by leaf-level environmental sensitivity and within-plant homogenization triggered by perception of the surroundings at plant-level. Both light attenuation, stimulating an increase of morphological variability, and nutrient surplus, initiating the stabilization of morphological parameters, could have adaptive advantages. The variability of leaf size leads to diversification of foliar parameters, thus increasing the efficiency of light harvest at low-nutrient sites and making responses to changes in the light environment more dynamic. These results suggest that leaf-level-induced diversification is counteracted by the standardization effect triggered by plant-level environmental factors.

Key words: Potamogeton / within-plant variability / morphology / nutrient / light

Introduction

By way of phenotypic plasticity, a plant genet produces different morphological forms according to the environmental conditions present. This prevents the decrease of its fitness and therefore has an evolutionary function. Many studies recognize the adaptive role of phenotypic plasticity in plant species (Wells and Pigliucci, 2000; Miner *et al.*, 2005; Garbey *et al.*, 2006), and only recently ecological and evolutionary importance of plastic interaction between individual organisms and their environments has also been recognized (De Kroon *et al.*, 2005; Barthélémy and Caraglio, 2007; Karban, 2008).

Little is known about the importance and ecological function of within-plant morphological variability (Orians and Jones, 2001). Previous morphological studies mainly focus on variability along major environmental transitions

resulting in some important developmental (heteroblastomy) or ecological (heterophylly) changes (Wells and Pigliucci, 2000), but less drastic environmental gradients have not been studied at all, even though they might add substantially to the understanding of the transition from acclimation to adaptation.

Owing to the fact that it is built from somatic modules that appear during ontogenesis, repeatedly recreating the same pattern of vegetative tissue (*e.g.*, leaves, internodes, etc.), a single plant is sensitive to its environment at the whole-plant, as well as sub-individual (leaves, internodes, etc.) levels. At the location of a plant some environmental factors (*e.g.*, light in the tree crown or light attenuation within the water column) change in a spatially deterministic way, thus each leaf perceives a unique environmental signal from the conditions present. Moreover, the effect of these local conditions are expressed over a very limited distance such that the light perceived by a *Potamogeton* leaf will manifest within that specific leaf (hereinafter

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referred to as leaf-level environmental conditions), thus increasing the heterogeneity of plants. In addition to these leaf-level environmental signals, the whole plant also perceives environmental signals that have general effects on the whole plant (*e.g.*, chemical or physical characteristics of the sediment – hereinafter referred to as plant-level environmental conditions). It is not known how the plant-level and leaf-level environmental factors operate, but it could be presumed that plant-level environmental factors would affect the whole plant in general, while sensitivity to environmental factors at the single leaf-level would manifest within a single plant in high morphological variation of its somatic modules (De Kroon *et al.*, 2005; Schlichting and Piglucci, 1998). Late environmental acclimatization at subindividual level affects the performance of a single plant, helping individual plants exploit all possible slices of environment, while the decrease of subindividual variability might lead to specification of the plant to the given environmental conditions. Therefore, it is possible that within-plant variability of different morphological parameters could have evolutionary consequences.

Macrophytes are especially suitable for examining not just plant-level, but also within-plant heterogeneity, as they experience much stronger vertical gradients (especially light, within the water column) than terrestrial plants. For this, we used a common and wide-spread plant, *Potamogeton perfoliatus* L., which is highly variable; therefore it is to be expected that it will show changes in its morphology and within-plant morphological variability to environmental factors, in the present case to the very much differing conditions at study sites around the lake, constituting therefore a suitable model for examining how a single macrophyte can react to changes in the environment.

Lake Balaton is large (596 km²), shallow (mean depth: 3.5 m) and elongated in shape. Its northern, windward shore has a constant, rather steep depth gradient, its sediment consisting of more nutrient-rich dolomite limestone, whereas the southern shore is shallow and mildly sloped with a sandy bottom, which is more wave exposed (Máté, 1985). These differences result in shore-specific light environments: the deeper northern shore, owing to higher light attenuation has a lower average irradiance and a vertically more heterogeneous light environment (seasonal average of irradiance at basal leaf < 10 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), while the shallow, more transparent southern shore has a sunnier and a vertically more homogeneous light environment (seasonal average of irradiance at basal leaf ca. 250 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) (Tóth *et al.*, 2011). In addition to the difference in light environment, there is a west-east trophic gradient due to the only large inflow at the westernmost basin of the lake. The river Zala constitutes a major source of external nutrient loading at the westernmost basin, resulting in a eutrophic state of the basin, while the easternmost basin of Lake Balaton is mesotrophic (Présing *et al.*, 2008).

The objective of this study was to investigate within-plant variability of light-sensitive morphological

parameters on leaves and stem, and its relation to shore-specific light and basin-specific trophic environments. The hypothesis of the study was that plant-level environmental conditions (*i.e.*, nutrient levels) decrease the variability of morphological features leading to homogenization, whereas leaf-level environmental signals increase heterogeneity (*i.e.*, morphological variability), thus leading to diversification. The interaction (synergism, antagonism and amplification) of the plant-level and leaf-level environmental conditions on morphological variability were also studied in this experiment: could environmental effects at different levels act together (synergism), or act against each other (antagonism), or could the magnitude of one (or both) environmental conditions be amplified by the other (amplification)?

Materials and methods

Sampling sites

Lake Balaton exhibits major trophic gradient (west-to-east) and shore-specific (northern *vs.* southern) light environment, thus study areas were chosen so as to reflect these differing conditions. Nine sampling points within highly vegetated areas were chosen (Fig. 1): about half of the sites were on the southern and half on the northern shore, and about half were in the easternmost basin and about half in the westernmost basin.

Chemical characteristics of the sediment were obtained from Csermák and Máté (2004), and also validated by our own measurements at nine points according to Buzás (1988). The data of Csermák and Máté (2004) are shown in Table 1a.

The specific light environment was measured with pendant light sensors (Onset Corp., USA) for every 20 cm throughout the entire depth of the water column at each sampling site. Measurements in the westernmost basin were performed once a month throughout the vegetation period at multiple points with seven sensors fixed to a plastic pole, whereas in the easternmost basin the light was measured throughout the whole vegetation period with fixed sensors. The light attenuation coefficient (K_d) of the sampling sites was calculated based on these data. Results of the light measurements are summarised in Table 1b.

Plant sampling and measurements

Sampling took place in July and August, 2007. At each sampling point, between four and six intact, healthy looking *P. perfoliatus* shoots were collected at random and transported in a cooling box to the laboratory.

All leaves and internodes of every shoot were measured. Parameters reflecting the shape and size of leaves (leaf length, leaf width, leaf area and leaf dry weight) were measured. Leaves were scanned and their dimensions acquired using the software ImageJ

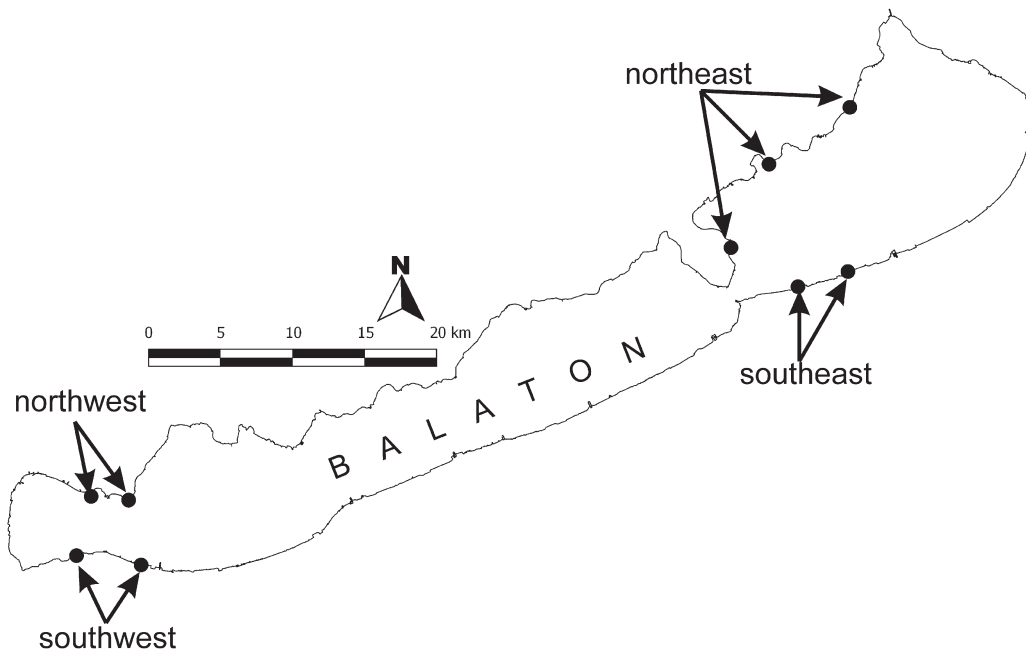


Fig. 1. Schematic view of the sampling sites in Lake Balaton.

Table 1a. Water depth (cm), light attenuation coefficient of whole water column (m^{-1}) and the number of samples at the north-eastern (NE), south-eastern (SE), north-western (NW) and south-western (SW) study sites of Lake Balaton (average \pm SD). Different letters after the numbers show statistically different results ($P < 0.05$).

	NE	SE	NW	SW	Samples
Depth	143 ± 6^a	83 ± 3^b	125 ± 10^a	79 ± 4^b	4
K_d	2.2 ± 0.3^a	1.9 ± 0.2^a	3.3 ± 0.3^b	2.6 ± 0.3^b	> 8

Table 1b. Total phosphorus ($mg\ kg^{-1}$), total nitrogen ($g\ kg^{-1}$), $CaCO_3$ (%) content and pH of the sediment at the north-eastern (NE), south-eastern (SE), north-western (NW) and south-western (SW) study sites of Lake Balaton (average \pm SD). Number of samples: 4. For more information please see Csermák and Máté (2004). Different letters after the numbers show statistically different results ($P < 0.05$).

	NE	SE	NW	SW
Total P	143 ± 46^a	50 ± 21^b	204 ± 13^c	234 ± 32^c
Total N	2.2 ± 0.1^a	0.5 ± 0.1^b	10.0 ± 7.7^a	5.9 ± 3.4^a
$CaCO_3$	48 ± 8^a	20 ± 4^b	54 ± 1^a	35 ± 7^c
pH	7.2 ± 0.1^a	7.6 ± 0.3^b	7.6 ± 0.1^b	7.2 ± 0.1^a

(<http://rsb.info.nih.gov/ij/>). Leaves were dried at $105^\circ C$ to a constant weight and weighed. Within-plant morphological variability was calculated for each single plant as the difference between the maximal and minimal values of that parameter relative to the minimum of that same parameter ($[(\max - \min) / \min]$).

Data analysis

The nutrient effect was calculated as the difference between the morphological parameters between the westernmost (eutrophic) and easternmost (mesotrophic) basins. In analogy, the difference in morphological parameters between the northern and southern shores of Lake Balaton was postulated as the light effect.

For the General Linear Model (GLM) test, morphological and variability data were tested with the shore (light) and the basin (nutrients) as categorical variables, water depth and the date (day from 1st of January) of sampling as continuous variables and plants as random variables. Normality of error and homogeneity of variance were checked and necessary transformations were applied. Measured variables were tested with a *t*-test, a GLM and Spearman correlation using RExcel (Baier and Neuwirth, 2007).

Results

Both nutrient and light environment significantly affected the appearance of *P. perfoliatus* leaves. The largest

Table 2. Leaf number, leaf area (LA – cm²), leaf width (width – cm), leaf length (length – cm), leaf dry weight (DW – mg) and internode length (internode – cm) (average ± SD) of *P. perfoliatus* at the north-eastern (NE), south-eastern (SE), north-western (NW) and south-western (SW) study sites of Lake Balaton (average ± SD) and the effect of nutrients (i.e., difference between the western and eastern basins) and light environment (i.e., difference between the northern and southern shores) of these parameters (*t*-test). *n* – number of measured parameters.

<i>n</i>	NE 1233	SE 895	NW 647	SW 458	Effect of nutrients	Effect of light
Leaf number	25.4 ± 9.3	24.0 ± 6.7	22.4 ± 13.1	26.3 ± 9.4	6% ^{ns}	– 4% ^{ns}
LA (cm ²)	5.4 ± 2.5	4.2 ± 2.1	7.8 ± 3.9	6.4 ± 2.6	29% ^{***}	15% ^{***}
Width (cm)	2.1 ± 0.6	1.9 ± 0.6	2.3 ± 0.6	2.2 ± 0.5	9% ^{***}	6% ^{***}
Length (cm)	3.4 ± 0.8	2.8 ± 0.7	4.6 ± 1.2	3.9 ± 0.9	25% ^{***}	11% ^{***}
DW (mg)	12.5 ± 6.8	12.1 ± 7.1	22.3 ± 15.9	15.7 ± 6.9	33% ^{***}	9% ^{***}
Internode (cm)	2.8 ± 1.7	1.3 ± 0.6	3.0 ± 2.6	2.5 ± 1.4	19% ^{***}	38% ^{***}

The significance of *t*-test: ns → $P \geq 0.05$, *** → $P < 0.001$.

Table 3. Effect of nutrients and light on leaf area (LA), leaf width (width), leaf length (length), leaf dry weight (DW) and internode length (internode) of *P. perfoliatus* in Lake Balaton. Morphological parameters were tested with the shore (effect of light) and the basin (effect of nutrients) as categorical variables, water depth and the date (day from 1st of January) of sampling as continuous variables and plants as random variables. Numbers are *F*-values of the GLM test. All results were significant at $P < 0.001$.

	Effect of nutrients	Effect of light
LA	552.3	77.5
Width	104.7	38.0
Length	1361.0	168.3
DW	382.1	27.4
Internode	179.5	267.3

and heaviest leaves were obtained at the north-west sampling points, where both the high nutrient (total N and total P, Table 1b) and the heterogeneous irradiance (K_d , Table 1a) influenced leaf morphological parameters (Table 2), whereas the plants at the south-east site (lowest nutrient and the most homogeneous light environment) had the smallest leaves (Table 2). The effect of nutrient content of the sediment was more pronounced, since all foliar parameters were on average 24% higher in the nutrient-rich westernmost basin, while the more heterogeneous light environment of the northern shore increased all foliar parameters by ca. 10% (Table 2). Besides the foliar parameters, the internode length was also highest at the north-western site and lowest at the south-eastern site, but the influence of light heterogeneity was more pronounced (38%), than that of nutrient content (19%, Table 2). The GLM test also supported the fact that the trophicity of the studied sites predominantly influences the foliar parameters, while the heterogeneity of light had a more pronounced influence on internodal length of *P. perfoliatus* (Table 3).

Foliar parameters of *P. perfoliatus* increased with increasing nutrient content of the sediment: for example, the leaf area of plants ranged from 4.2 to 7.8 cm² (~86% increase), whereas leaf biomass varied from 12.1 to 22.3 mg (DW) (~84% increase), although significant

correlations were only found with total nitrogen content (Fig. 2, Table 4). The increase in leaf size with increasing total nitrogen content of the sediment was coupled with a decrease of within-plant morphological variability of the studied parameters (Fig. 2, Table 4).

Thus, the highest within-plant variability of foliar parameters was obtained in south-eastern sites, where the smallest leaves were measured on average, while the lowest within-plant variability of foliar parameters was calculated for the north-western sites, characterised by the largest leaves (Tables 2 and 5). Overall, within-plant morphological variability of foliar parameters was reduced by half as a result of nutrient enrichment in the western basin, while light had no significant effect on within-plant variability of foliar parameters (Table 5). Meanwhile, the only non-foliar parameter (internode length) showed neither nutrient, nor light related changes in within-plant variability (Table 5). The GLM test supported these results: only nutrients affected within-plant variability of foliar morphology, while the effect on internode length was not significant (Table 6).

The trade-off between the number of leaves and the average leaf area of plants showed a gradual decrease at all study sites, although with very low correlation factors (0.06–0.43) and only in the north-eastern (NE) study site was this correlation significant (Fig. 3). The light environment affected this trade-off, since the study sites with more heterogeneous light environments had higher correlation factors (0.31 and 0.43), than sites with more homogeneous light environments (0.06 and 0.08) (Fig. 3).

Discussion

Foliar and habitual morphological parameters that are well-known for their ability to respond to irradiance were studied *in situ* in Lake Balaton. The results showed that even the light-sensitive parameters are more influenced by nutrient availability than by light intensity: nutrient surplus in the sediment increased the size of leaves as has been described in numerous previous studies (Moore and Wetzel, 2000; Crossley *et al.*, 2002; Cronin and Lodge, 2003; Vári *et al.*, 2010), although in our case *P. perfoliatus*

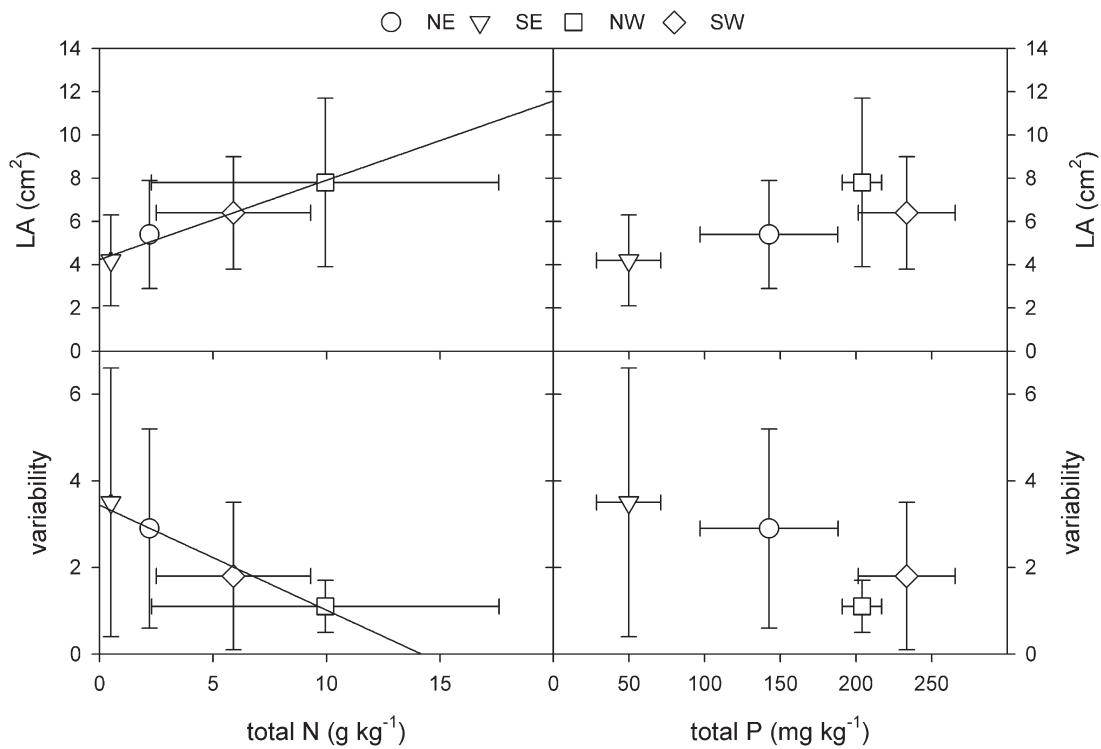


Fig. 2. Effect of total N (g kg^{-1}) and total P (mg kg^{-1}) contents of sediment on the leaf area (LA, cm^2) and on within-plant morphological variability of *P. perfoliatus* in the north-eastern (NE), south-eastern (SE), north-western (NW) and south-western (SW) sampling points of Lake Balaton. Each symbol represents the average \pm SE (n at least 22). Lines shown depict significant correlation ($P < 0.05$, also see Table 4).

Table 4. Results of linear correlation (R^P) of leaf area (LA), leaf width (width), leaf length (length), leaf dry weight (DW), internode length (internode), leaf number and their variability ($[\text{max}-\text{min}]/\text{min}$) with total nitrogen and total phosphorus of the sediment at the study sites.

	Total N	Total P
Morphological data		
LA	0.99*	0.85 ^{ns}
Width	0.94 ^{ns}	0.92 ^{ns}
Length	0.99*	0.85 ^{ns}
DW	0.97*	0.65 ^{ns}
Leaf number	-0.34 ^{ns}	0.24 ^{ns}
Internode length	0.73 ^{ns}	0.78 ^{ns}
Morphological variability		
LA	-0.99*	-0.88 ^{ns}
Width	-0.95*	-0.84 ^{ns}
Length	-0.94 ^{ns}	-0.96*
DW	-0.99**	-0.88 ^{ns}
All foliar	-0.99**	-0.87 ^{ns}

The significance of correlation: ns $\rightarrow P \geq 0.05$, * $\rightarrow P < 0.05$, ** $\rightarrow P < 0.01$.

was only significantly influenced by total nitrogen. Average light intensity of the studied sites also influenced the growth of leaves and spatial distribution of internodes: at more shaded sites larger leaves and longer internodes were found, as found by other studies and our previous

results (Cenzato and Ganf, 2001; Cronin and Lodge, 2003; Vári *et al.*, 2010; Tóth *et al.*, 2011).

Our results show that the variability of foliar parameters was probably induced by light, and more precisely by vertical heterogeneity of irradiance within the water column. Nevertheless, this morphological heterogeneity was significantly diminished as an effect of higher nutrient availability.

Light, as one of the spatially most variable environmental factors, is absorbed by different tissues (mostly leaves) of *P. perfoliatus* at different intensities. This light, absorbed by a leaf, could 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 (Vári *et al.*, 2010; Tóth *et al.*, 2011), showing in high within-plant morphological variability as in this study. In nutrient-limited conditions, *P. perfoliatus* shows a non-conservative resource-use strategy for morphological traits (Vári *et al.*, 2010; Tóth *et al.*, 2011), allowing for the plant to adapt to the actual light environment, not only at the plant-level, but, as the present study also shows, also at the leaf-level. In a vertically heterogeneous light environment, it is advantageous for *P. perfoliatus* to have higher morphological variability as this will result in a greater flexibility of responses and more effective light capture. This fine-tuning cooperation of flexibility and effectiveness results in differential placement of leaves with different photosynthetic areas within the canopy for sustainable photosynthesis: as an acclimation to the lower light

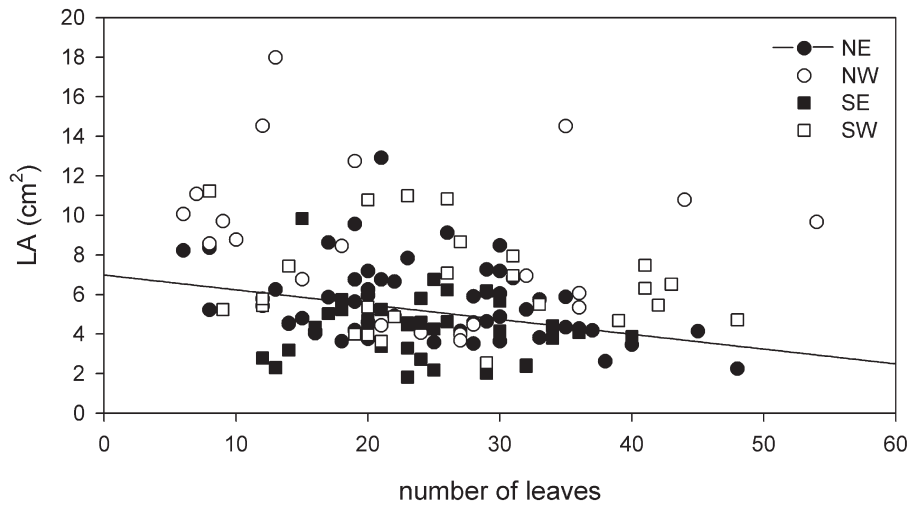


Fig. 3. Relation between the number of leaves and the average leaf area (LA – cm²) of *P. perfoliatus* at the north-eastern (NE), north-western (NW), south-eastern (SE) and south-western (SW) study sites of Lake Balaton. Line depicts significant correlation ($R = 0.42$) at $P = 0.014$.

Table 5. Within-plant morphological variability ([max–min]/min) of leaf area (LA), leaf width (width), leaf length (length), leaf dry weight (DW) and internode length (internode) of *P. perfoliatus* at the north-eastern (NE), south-eastern (SE), north-western (NW) and south-western (SW) study sites of Lake Balaton (average \pm SD) and the effect of nutrients (i.e., difference between the western and eastern basins) and light environment (i.e., difference between the northern and southern shores) of these parameters (*t*-test). *n* – number of studied plants.

	NE	SE	NW	SW	Effect of nutrients	Effect of light
<i>n</i>	54	39	22	25		
LA	2.9 \pm 2.3	3.5 \pm 3.1	1.1 \pm 0.6	1.8 \pm 1.7	– 117%***	– 17% ^{ns}
Width	1.2 \pm 0.7	1.2 \pm 0.5	0.7 \pm 0.4	0.8 \pm 0.4	– 63%***	4% ^{ns}
Length	0.9 \pm 0.7	1.2 \pm 0.8	0.5 \pm 0.3	0.6 \pm 0.5	– 84%***	– 21% ^{ns}
DW	4.3 \pm 4.8	5.2 \pm 4.9	1.6 \pm 0.9	2.7 \pm 2.8	– 119%***	– 19% ^{ns}
Foliar average	2.4 \pm 0.2	2.7 \pm 0.3	1.0 \pm 0.1	1.5 \pm 0.2	– 106%***	– 15%^{ns}
Internode length	7.1 \pm 6.7	4.7 \pm 5.2	4.9 \pm 5.3	8.0 \pm 9.8	7% ^{ns}	7% ^{ns}
All parameters	2.9 \pm 0.3	2.8 \pm 0.3	1.6 \pm 0.2	2.4 \pm 0.2	– 41%***	– 5%^{ns}

The significance of *t*-test: ns \rightarrow $P \geq 0.05$, *** \rightarrow $P < 0.001$.

environment, larger leaves are grown at the shadier, basal part of the plant, while smaller, but physiologically more efficient leaves concentrate at the apical, well-lit region of *P. perfoliatus*, thus minimizing self-shading. The light-dependent growth of internodes also concentrate the majority of foliar biomass in the optimal light environment, the internode length is higher at the basal and lower in the apical regions of *P. perfoliatus*.

Although this sort of within-plant morphological variability is a result of interaction between both intrinsic (developmental stage and sectoriality) and extrinsic (abiotic and biotic) factors (Wells and Pigliucci, 2000; Orians and Jones, 2001; De Kroon *et al.*, 2005), our results show that it could be significantly altered. The homogenization (decrease of variability) of foliar morphology by nutrient surplus (a plant-level environmental factor) shows its antagonistic impact, counteracting the differentiating effect of the present leaf-level stimuli of light. Unlimited amount of nutrients increases the metabolism of plants, and consequently neglects the differentiating effect of light attenuation: production and growth of leaves,

Table 6. Effect of nutrients and light on variability of morphological parameters of *P. perfoliatus* of Lake Balaton. Variability of morphological parameters were tested with the shore (effect of light) and the basin (effect of nutrients) as categorical variables, water depth and the date (day from 1st of January) of sampling as continuous variables and plants as random variables. Numbers are *F*-values of the GLM test, while in the uppercase is the significance of the test, where ns – not significant, and *** is $P < 0.001$.

	Effect of nutrients	Effect of light
LA	17.47***	2.36 ^{ns}
Width	22.82***	0.56 ^{ns}
Length	16.86***	2.59 ^{ns}
DW	11.06***	3.7 ^{ns}
Internode length	0.23 ^{ns}	0.01 ^{ns}

influenced by hormonal activity of the plant apex and existing leaf primordia, is overridden by physiological and hormonal changes in the root tips, triggered by the surplus of nutrients. It might work by analogy as adaptive

phenotypic plasticity counteracts the ecotype-like specialization of plants to a given environment (Sultan, 2000; De Jong, 2005; Funk *et al.*, 2007).

It was shown that morphology of plants could be shaped by two counteracting forces at the same time: differentiation driven by leaf-level environmental factors and standardization controlled by plant-level environmental factors. Moreover, within-plant diversification also might have not only ecological as it enhances the range of environmental conditions the plant can endure, but also evolutionary significance as it influences the distribution area of the species in the long run (Orians and Jones, 2001; Orians *et al.*, 2002).

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