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Morphometric structural analysis of *Phragmites australis* stands in Lake Balaton

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Abstract – *Phragmites australis* is a stand forming emergent macrophyte that displays large phenotypic variation within Lake Balaton. The present study assesses morphological variations of *P. australis* within three transects of different reed stands of Lake Balaton which differ with respect to bathymetry, reed quality and geographic position in order to achieve a morphological typization. On average the southern stable stand produced the largest and thickest plants (295 ± 9 cm and 7.5 ± 0.2 mm), while plants of the northern die-back stand were approximately half this size (141 ± 2 cm and 3.5 ± 0.1 mm). The slow growth and development of Phragmites characterizing the northern die-back stand was the result of fewer and shorter internodes, which also resulted in the low number of green leaves. The most influential factor shaping the phenotypic properties of the plants was determined to be the reed quality (general condition), although site-specific differences, shore-specific differences, water depth and spatial position within reed stand transects were also found to be significant. Despite the differences in the studied stands and almost certain genetic dissimilarities, three morphological ecotypes of Phragmites were distinguished on the basis of stem height to basal diameter ratio, stem density and phenotypic plasticity of plants. These ecotypes were primarily correlated to water depth at their position within the reed stand. The similarity of the spatial distribution of stem heights to basal diameter ratios and phenotypic plasticity of plants along all studied reed stands suggests that morphological typization should be considered to provide additional information on ecological zonation of stands.

Key words: *Phragmites* / morphology / integration / zonation / ecotypes

Introduction

Due to its high adaptability, *Phragmites australis (Trin. ex Steud.)* is able to monopolize littoral zones and become the dominant species (Clevering, 1998; Kühl *et al.*, 1999; Bart and Hartman, 2000; Vretare *et al.*, 2001; Hansen *et al.*, 2007; Englоner, 2009). *Phragmites* is characterized by high growth rates and predominantly clonal vegetative reproduction. Self-seeding in *Phragmites* stands is impossible in water covered areas, the spatial distribution of their shoots (ramets) is mainly determined by the spread of rhizomes. Reed structure is affected by two counteracting processes. On the one hand, the plants tend to remain as dense as possible preventing the intrusion of competitors. On the other hand, the density of the rhizome is optimized for the most efficient interception and utilization of resources. Thus, abiotic and biotic factors of a given habitat both significantly affect the zonation of reed stands (Vretare *et al.*, 2001; Santamaría, 2002).

One of the most important structuring features of clonal *Phragmites* is the physiological integration of genets (clones), which facilitates intraclonal cooperation (Pitelka and Ashmun, 1985; Hara *et al.*, 1993; Amsberry *et al.*, 2000), and thus substantially influences competition within a reed stand. Biotic and abiotic factors, together with predominantly vegetative reproduction shape the borders between clones within a reed stand (Ailstock and Center, 2000; Santamaría, 2002). Basic morphological units of *Phragmites* (ramets) are not considered a discrete entity due to physical (and thus physiological) interconnections with other ramets via associated rhizomes. The interconnected clone represents the basic physiological unit of *Phragmites*, which is able to independently interact with the given environment (Pitelka and Ashmun, 1985; Hara *et al.*, 1993; Amsberry *et al.*, 2000). This hierarchical structure of reed stands is well established, but is often overlooked in morphological studies.

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As a result of the rationalized distribution of nutrients and photosynthates within a clone, the physiological interaction of ramets leads to the standardization of morphological properties: ramets in need and growing shoots are supported by plants with greater access to resources (Pitelka and Ashmun, 1985; Hara *et al.*, 1993; Amsberry *et al.*, 2000). Although this is not a reed-specific feature (Stueffer *et al.*, 1996; Schwinning and Weiner, 1998; Oborny *et al.*, 2000), *Phragmites* is one of the few species that is able to efficiently exploit the capabilities of physiological integration and thus grow in monocultures. In the absence of high disturbance, this results in the uniform appearance of stands: great majority of the plants within the clone have the same size. The distance at which this size standardization takes effect depends primarily on the size of each clone and can be quite a large area (Neuhaus *et al.*, 1993; Keller, 2000; Koppitz and Kühl, 2000), although at the edges of the clones due to interclonal competition the standardization is defied. Thus, sampling within a smaller area could result in a dependent sampling and as such could result in erroneous data.

Lake Balaton is a large (596 km^2) and relatively shallow (average water depth 3.5 m) lake. In Lake Balaton reed is the stand forming helophytic perennial of the littoral zone and is commonly found in extended, continuous populations along 112 km of the 254 km shoreline. The total area of reed stands of Lake Balaton is *ca.* 16 km^2 and the majority (73% – *ca.* 12 km^2) of it is located on the northern shore. The windward, steep northern shore's sediment consists of dolomite limestone, while the shallow, southern shore is dominated by sandy sediment. On the northern shore of Lake Balaton reed can be found in up to 2.4 m deep waters (average waterward depth of the stands is 1.5 m), while on the southern shore the average depth at waterward side of stands is 1 m.

Previous studies showed that *Phragmites* have very high phenotypic variability in Lake Balaton (Tóth *et al.*, 1963; Herodek and Tóth, 2003, 2004; Engloner and Papp, 2006). However, these studies concentrated on the comparison of morphological parameters collected from discrete sampling points of distant studied sites. More recent studies show the high genetic diversity of *Phragmites* along the waterward-terrestrial transect stands of Lake Balaton with increasing variability towards the terrestrial side (Englone*r et al.*, 2010; Englomer and Major, 2011).

Phenotypic plasticity of reed has been studied as a function of some environmental conditions (Hutchinson, 1975; Vretare *et al.*, 2001), or the presence of another species (Armstrong and Armstrong, 2001; Bellavance and Brisson, 2010), but plasticity in response to intraspecific competition in a monospecific reed stand has never been estimated. Due to its clonal nature, intraspecific competition of *P. australis* differs significantly from that of non-clonal plants (Makita, 1996; Oborny *et al.*, 2000) and could result in significantly different morphological and physiological adaptation mechanisms that ought to be studied.

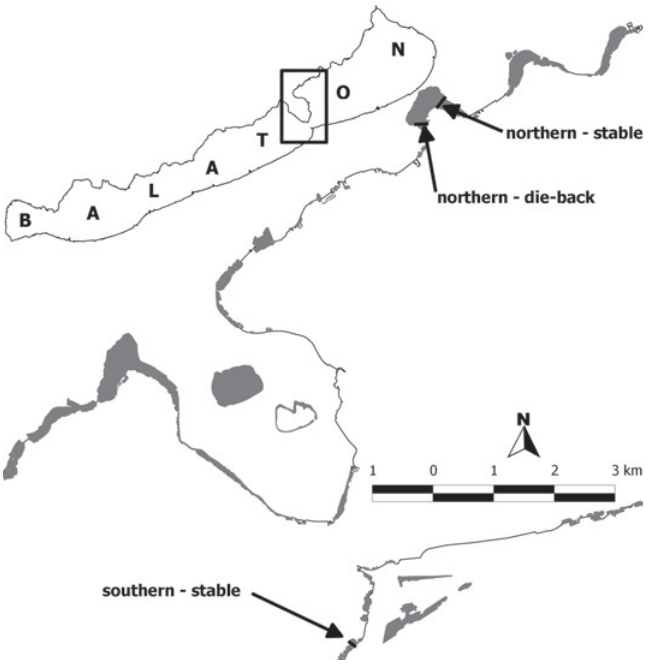

Fig. 1. Schematic map of the sampling sites in Lake Balaton. The reed belt of Lake Balaton is shown in grey.

This paper presents results of a morphometric field study of common reed (*P. australis*) performed in 2006 on stable and die-back reed stands of the northern shore of Lake Balaton and a stable stand of Lake Balaton's southern shore. To minimize site specific effects, transects of a similar length, plant community composition, developmental stage, age and length of water coverage were chosen. Our objectives were to determine the spatial dynamics of morphological parameters of common reed in transects between the waterward and terrestrial edges of the stands and to better understand the zonation of phenotypic factors within reed stands.

Materials and methods

Description of study areas

Study sites were chosen on the northern and southern shores of the Lake Balaton. On the northern shore one stable (46°58'3.11"N, 17°55'12.62"E) and one die-back (46°57'50.95"N, 17°55'0.28"E) stand were chosen. One stable stand was selected on the southern shore, situated close to the village of Szántód (46°51'58.92"N, 17°53'52.88"E) (Fig. 1). The stable northern stand was characterized by tall and thick reeds, homogeneously distributed all over the north-eastern side of the Kerekedi-Bay of Lake Balaton. Clumping, shorter and thinner reeds characterized the die-back stand on the western side of the same bay *ca.* 460 m apart (Fig. 1). One hundred and fifty-three and 157 m transects were chosen at the stable and die-back sites of the northern shore, respectively, with some minor inter-site bathymetric

Table 1. Water depth (cm) at the stable and die-back stands on the northern shore and on the southern shore of Lake Balaton at the time of sampling. Beyond 110 m there were no water covered areas in any of the sites.

Metres	Northern-stable	Northern-die-back	Southern-stable
0	150	165	90
10	135	115	85
20	30	35	55
30	15	15	25
40	10	15	15
50	10	15	15
60	5	10	15
70	5	10	10
80	5	5	5
90	–	5	5
100	–	5	–
110	–	5	–

differences (Table 1). The age of the reed stand at the Kerekedi-Bay is difficult to estimate, but at its earliest known depiction on the Krieger map (1776) of Lake Balaton, the area was already filled with reed (Bendefy and Nagy, 1969). Over time the extent of the reed stand in this area has changed significantly and was mostly influenced by the long-term water level. At the time of this study, lake water level had been kept artificially stable for more than 3 years.

The reed stand of the southern shore consisted of homogeneous, tall, thick reeds, somewhat sparsely distributed along the transect. The reed stand of the southern shore is much younger in comparison with that of the northern shore, however, even the most recent reed stand to appear on the southern shore is at least 60–70 years old. All sites are close to urban areas (within 200 m on the northern and within 50 m on the southern) with no agricultural activity (a pasture on the northern shore with no fertilization), relatively low suburban traffic and moderate recreational disturbance in general (angling for the most part). The reedbeds at the time of sampling were not exploited for at least the past 9 years.

The water level in Lake Balaton, particularly during the 3 years prior to the study, was artificially stabilized, resulting in an average annual fluctuation of 37 cm ($<11\%$). The highly regulated water level of the lake stabilized the bathymetric differences between the stands: on the northern shore the maximal depth of *Phragmites* progression was higher (150 and 165 cm on the stable and die-back stands, respectively), than on the southern shore (90 cm) (Table 1). Despite this, all three stands show very similar bathymetric structure: part of each transect, usually the first 20–30 m, was situated in water deeper than 15 cm, while the terrestrial (not covered with water, but still waterlogged) part of the transects started at 90–110 m.

Morphological measurements

To ensure no developmental differences would occur, the survey took place between August 12 and 28, 2006, at the climax stage of reed development. At each chosen site a transect was selected, extending from the terrestrial to the waterward edge of the reed stand. Transects were selected based on their comparable size (153–165 m in length), similar developmental stage and similar plant composition (mostly monospecific reed).

Plants were sampled every 5–20 m. At each sampling point, four 25 × 25 cm quadrants were randomly placed within 2 m of each other and all reed plants within the sampling quadrant were harvested at the connection of stems to horizontal rhizomes (under water at some points). The harvested reed was separated into dry and green, and only the green stems were used for further biometric measurements.

Stem height was determined from cut surface to the tip of the top leaf with a measuring tape. The diameter in the middle of the basal internode of each reed stem was measured with a vernier calliper. Green and dry leaves of each plant were counted, as were number of nodes and stems.

Phenotypic plasticity of a certain morphological parameter was calculated for each single plant as the difference between the maximal value and the minimal value of that parameter relative to the minimum of that parameter ([max–min]/min). Overall phenotypic plasticity of plants at a sampling point was averaged for each morphological parameter separately.

Sediment analysis

Sediment sampling was performed at four points along each transect: before the reed stand ("water"), at the waterward edge of the reed stands ("edge"), in the middle of the studied stand ("middle") and at the terrestrial side of the stand ("dry"). Sediment samples were collected with 500 mm long, 60 mm (53 mm inner) diameter plastic tubes and the upper 20 cm of the sediment was used. At each sampling point, three sediment cores were collected. All chemical and physical measurements were performed according to Buzás (1988). Part of the collected sediment was digested using an HNO_3-H_2O_2 mixture. Half of the resulting aliquot was used for total phosphorus determination (ammonium–molibdenate and ammonium–metavanadate colourimetric method), while the other half of the aliquot was used for total potassium determination with atomic absorption spectrophotometer in emission mode. Part of the sediment was digested using phenol–sulfuric acid and total nitrogen measured following the macro-Kjeldahl method. $CaCO_3$ content of the sediment was measured through the CO_2 release after treatment with 10% hydrochloric acid. Humus content was measured on a photometer following the sulfuric acid–potassium dichromate digestion of the organic C content after calibration for glucose and the humus content was calculated using the following equation: humus = 1.724* organic C. Ignition loss was determined gravimetrically following gradual heating to 550 °C ($CaCO_3$ content of the samples was taken into consideration). Water capacity of sediment samples was measured as the upper limit of plasticity of the dried and then re-watered samples with the following typical texture classes:

Coarse sand	< 25 mL/100 g sediment
Sand	25–30 mL/100 g sediment
Sandy loam	31–37 mL/100 g sediment
Loam	38–42 mL/100 g sediment
Clay loam	43–60 mL/100 g sediment
Clay	51–60 mL/100 g sediment
Heavy clay	81–90 mL/100 g sediment

Sediment pH was measured five times in close proximity to the predefined points of each transect with a pH electrode with elongated cable.

Graphing and statistical analysis

Morphological parameters between stands were compared using the Tukey–Kramer test for one-way layout design. Correlation between measured morphological parameters was tested using the Spearman test. A general linear model (GLM) test of reed morphological data as dependent variables, shore (northern versus southern), quality (die-back versus stable) and site as conditional factors, plant as a random parameter and transect position and water depth as continuous factors was performed. Assumptions of normality and homoscedascity were tested and, when necessary, data were transformed to attain a normal distribution.

Data of height to basal diameter and phenotypic plasticity were interpolated using spline interpolation. This technique was favoured to decrease interpolation errors and also to use high degree polynomials. The goal of the interpolation was the discretization of studied parameters to predefined, equidistant transect points in order to standardize across transects. At spatial positions beyond the actual transect points (stands of the northern shore) data were extrapolated using the same degree of polynomials used as in spline interpolation from the original set of data. The data at these points were averaged (± SD) and visualized. All statistical analysis was performed using RExcel v.3.0.17 (Baier and Neuwirth, 2007). SigmaPlot 8.0 was used to graph results.

Results

The basic chemical and physical compositions and characteristics of the sediment from the northern stands were similar (Table 2). The sediment of the studied northern stands is dolomite limestone sediment typical of the northern shore of Lake Balaton with high water capacity, clay and silt content. The humus and organic content (measured by ignition loss) of the sediment was also elevated due to the presence of reed litter within the stands (Table 2). Northern stands' sediment had high N, P and K content. The southern shore stand is characterized by sandy sediment (minimal water capacity, low clay and silt content), with lower concentrations of organic content (humus and ignition loss) due to deposition of the litter at the foreshore. Nearly all nutritional parameters were also lower at the southern shore site compared with the northern shore sites (Table 2).

Bathymetric measurements within reed stands quantified the substantial differences between the northern and southern shores of Lake Balaton (Table 1). On the steep northern shore, *Phragmites* plants were found in deeper waters, thus at the waterward edge of the stands water depth was high (150 and 165 cm in the stable and die-back stands, respectively). The water level within 30 m into the transects is 15 cm. On the shallow southern shore, the water depth at the waterward edge of the stand was lower (~90 cm) and due to the mildly sloping bottom, 15 cm water depth was not reached until 40 m from the waterward edge of the stand (Table 1). Beyond 110 m of each transect, there were no water covered areas at any of the sites, although the soil was waterlogged throughout.

The average stem height on the southern shore of Lake Balaton was 295 ± 9 cm (average ± SE), while the average height of *Phragmites* of the stable stand on the northern shore was 274 ± 3 cm. The shortest plants were in the die-back, northern stand (141 ± 2 cm, Table 3). These differences were significant in all cases (at least $P < 0.01$, Table 3), but was greater or lesser depending on the specific spatial position (Fig. 2).

The spatial pattern of reed height in the waterward edge of the studied stands is similar between the stable (northern and southern) stands. Plant height at the first point of the transect was 30 and 70% (for northern and southern stable stands, respectively) lower than in the subsequent points. In the die-back site of the northern shore, the lack of *Phragmites* sprouts resulted in 25% higher stems at the edge than at the next point of the transect (Fig. 2A). At subsequent sampling points (from 2 to 10 m of the transect) northern stable stand stem heights were significantly higher (*ca.* 350 cm) than in the same spatial position of the northern die-back stand (*ca.* 120 cm) and the stable stand of the southern shore (*ca.* 300 cm) (Fig. 2A). From 20 m on, plants of the southern shore site reached their maximum height and were 404 ± 5 cm tall, while plants at the die-back site were the shortest (128 ± 7 cm). Towards the terrestrial end of all transects stem heights were similar to those of the waterward side (0 point of transect) (Fig. 2A).

The average basal diameters of *Phragmites* on the southern and northern stable shores of Lake Balaton were 7.5 ± 0.2 and 7.2 ± 0.1 mm (average ± SE). respectively, while the plants of the die-back northern stand were of smaller diameter (3.5 ± 0.1 mm) (Table 3, Fig. 2B). The stem diameters correlated with the height of plants (Spearman correlation, $R \sim 0.72–0.91$, $P < 0.001$, Table 4), thus the spatial distributions of basal diameters follow those described above for height (Fig. 2B).

Plants of the northern and southern stable stands had similar numbers of nodes on average (18 and 20, respectively), while *Phragmites* of the northern die-back stand had five fewer nodes on average (Table 3).

Table 2. Chemical and physical parameters of sediment at the northern and southern stands of Lake Balaton. In the table, the following abbreviation are used: water – stands for open water, "edge" – for the waterward edge of the reed stands, "middle" – for the middle of the transect, "dry" – for the terrestrials end of the transect, "nd" stands for "no data". Data shown are average of 3 replicates ± SD.

	Water	Edge	Middle	Dry
Northern stable				
pH	8.5 ± 0.1	8.4 ± 0.1	8.3 ± 0.1	8.5 ± 0.1
Humus (%)	5.4 ± 0.1	5.4 ± 0.1	5.4 ± 0.0	5.3 ± 0.0
Water capacity (ml)	97 ± 5	110 ± 7	95 ± 6	61 ± 6
Ignition loss (%)	20.5 ± 1.7	26.7 ± 0.7	26.6 ± 1.5	16.5 ± 0.7
$CaCO_3$ (%)	29.8 ± 4.3	27.7 ± 0.7	30.7 ± 1.7	6.4 ± 1.5
Clay + silt (%)	26.6 ± 0.9	27.5 ± 0.8	25.8 ± 0.8	25.6 ± 1.4
Total N (g.kg^{-1})	5.7 ± 0.2	7.6 ± 1.1	6.8 ± 0.5	1.8 ± 0.5
Total K (g.kg^{-1})	2.7 ± 0.6	4.3 ± 1.0	4.4 ± 1.0	4.9 ± 0.5
Total P (mg.kg^{-1})	209 ± 14	528 ± 88	567 ± 116	223 ± 42
Northern die-back				
pH	8.5 ± 0.1	8.2 ± 0.1	8.3 ± 0.1	8.5 ± 0.1
Humus (%)	5.5 ± 0.1	5.3 ± 0.1	5.4 ± 0.1	5.3 ± 0.0
Water capacity (ml)	107 ± 7	96 ± 10	95 ± 9	61 ± 7
Ignition loss (%)	23.8 ± 2.3	25.4 ± 1.0	23.7 ± 2.1	15.1 ± 1.0
$CaCO_3$ (%)	30.9 ± 0.8	36.2 ± 6.1	31.1 ± 1.4	6.8 ± 0.8
Clay + silt (%)	24.8 ± 1.3	26 ± 1.1	24.2 ± 1.1	24.1 ± 1.1
Total N (g.kg^{-1})	6.1 ± 1.1	5.4 ± 1.5	7.1 ± 1.2	2.8 ± 0.7
Total K (g.kg^{-1})	3.9 ± 0.8	4.1 ± 0.2	4.2 ± 0.2	5.9 ± 0.7
Total P (mg.kg^{-1})	183 ± 19	352 ± 125	336 ± 163	138 ± 59
Southern stable				
pH	8.3 ± 0.1	8.5 ± 0.2	8.3 ± 0.0	nd
Humus (%)	0.5 ± 0.1	0.89 ± 0.2	5.4 ± 0.7	5.9 ± 0.4
Water capacity (ml)	< 25	< 25	76 ± 13	nd
Ignition loss (%)	4.2 ± 1.3	1.9 ± 0.6	15.2 ± 6.0	78.1 ± 14
$CaCO_3$ (%)	18.3 ± 4.9	13.2 ± 4.3	22.1 ± 1.6	0.9 ± 0.1
Clay + silt (%)	2.1 ± 0.1	0.9 ± 0.2	6.5 ± 0.5	nd
Total N (g.kg^{-1})	0.3 ± 0.1	0.7 ± 0.3	4.6 ± 1.8	nd
Total K (g.kg^{-1})	1.5 ± 0.7	0.8 ± 0.3	2.9 ± 0.9	2.3 ± 0.5
Total P (mg.kg^{-1})	203 ± 14	147 ± 45	253 ± 28	565 ± 101

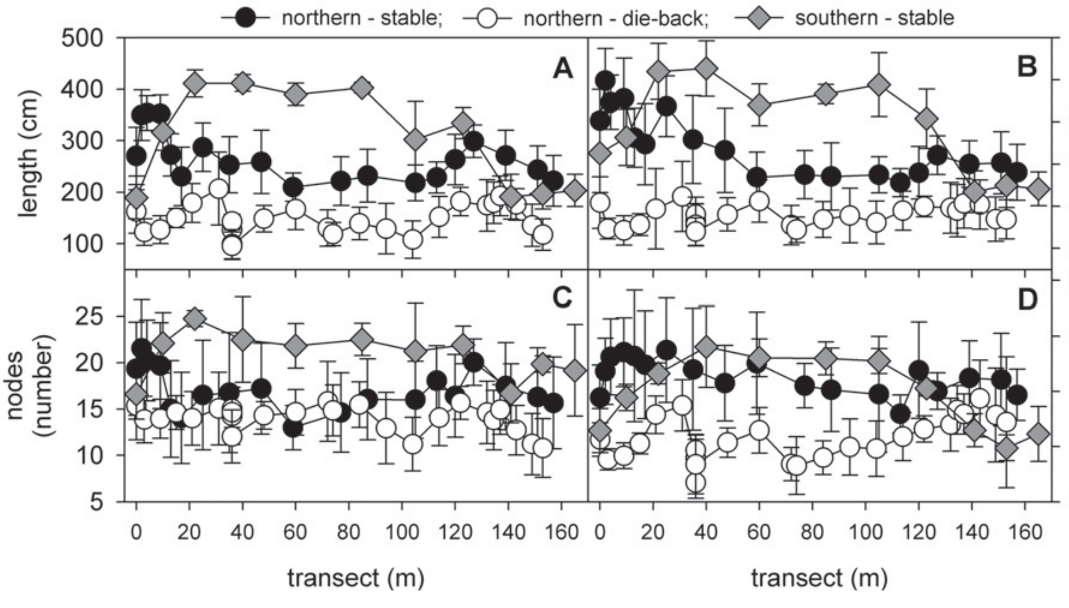

Fig. 2. Changes in morphological parameters of *Phragmites australis* along the stable (black symbols) and die-back (white symbols) stands of the northern shore and stable stands on the southern (grey symbols) shore of Lake Balaton. Each symbol represents average ± SD ($n = 14$–47).

Table 3. All transect averages of main morphologic parameters (average ± SE) of *Phragmites australis* from stable and die-back stands on the northern shore and the southern shore stands. Different letters after the numbers represent significant ($P < 0.01$) difference between the data determined using Tukey–Kramer test.

	Northern		Southern
	Stable ($n = 574$)	Die-back ($n = 595$)	($n = 132$)
Stem length (cm)	274 ± 3^{a}	141 ± 2^{b}	295 ± 9^{c}
Stem diameter (mm)	7.2 ± 0.1^{a}	3.5 ± 0.1^{b}	7.5 ± 0.2^{c}
Node number	18.0 ± 0.2^{a}	13.7 ± 0.1^{b}	20.3 ± 0.4^{c}
Internode length (cm)	15.9 ± 0.2^{a}	10.4 ± 0.1^{b}	14.4 ± 0.3^{c}
Green leaf number	13.3 ± 0.2^{a}	10.9 ± 0.1^{b}	13.6 ± 0.3^{a}
Dry leaf number	4.8 ± 0.1^{a}	2.7 ± 0.1^{b}	6.8 ± 0.2^{c}
Green/dry leaves	3.5 ± 0.1^{a}	5.2 ± 0.1^{b}	2.4 ± 0.1^{c}
Length/diameter (cm.cm^{-1})	395 ± 4^{a}	407 ± 4^{a}	396 ± 5^{a}
Stem density (m^{-2})	88.2 ± 8.9^{a}	49.4 ± 6.2^{b}	34.1 ± 2.8^{b}

Table 4. Spearman correlation between morphological parameters of *Phragmites australis* at the northern stable, northern die-back and southern stands of Lake Balaton. Coefficients and significances (R^{P}) of correlations are shown. P: ns→$P \geq 0.05$, *→$P < 0.05$, **→$P < 0.01$, ***→$P < 0.001$. For all tests n is from 132 to 595. Bolded coefficients show the $R > 0.6$.

	Length	Diameter	Dry	Green	Nodes
Northern-stable					
Diameter	**0.72*****				
Dry leaf number	**0.68*****	**0.66*****			
Green leaf number	0.52***	0.22***	0.12*		
Number of nodes	**0.71*****	0.41***	0.32***	**0.93*****	
Internode length	0.12*	0.24***	0.12*	**−0.69*****	− 0.58***
Northern-die-back					
Diameter	**0.79*****				
Dry leaf number	0.41***	0.35***			
Green leaf number	**0.61*****	0.46***	0.07^{ns}		
Number of nodes	**0.70*****	0.53***	0.47***	**0.90*****	
Internode length	**0.71*****	**0.61*****	0.13**	0.02^{ns}	-0.06^{ns}
Southern-stable					
Diameter	**0.91*****				
Dry leaf number	**0.65*****	**0.64*****			
Green leaf number	0.39***	0.27**	-0.01^{ns}		
Number of nodes	**0.70*****	**0.60*****	0.58***	**0.79*****	
Internode length	**0.80*****	**0.75*****	0.41***	-0.06^{ns}	0.21*

Nevertheless, major differences in the spatial distribution of node number between northern and southern stable stands were observed in the middle sections of the transects, where plants from the southern stand had consistently 8–9 more nodes than plants from the northern shore (Fig. 2C). These differences in stem length and node number resulted in similar average internode lengths in the stable northern and southern stands (15.9 and 14.4, respectively), while at the northern die-back site it was lower (10.4) (Table 3, Fig. 2C).

At the waterward end of the southern stand transect, *Phragmites* plants had 12 green and 4 dry leaves, but both significantly increased (50 and 150%) by 40 m into the stand, resulting in a decrease in the ratio of number of green to number of dry leaves (Fig. 3(A)–(C)). The number of green leaves gradually decreased towards the terrestrial end of the transect, while the number of dry leaves did not change between 5 and 11 m of the transect (Fig. 3(A) and (B)). The consistent change in number of green and dry leaves resulted in a very stable green to dry leaf ratio at the southern shore site, varying throughout the transect from 1.2 to 3.3 (Fig. 3(C)). The patterns of the spatial distribution of green and dry leaf numbers at the stable and die-back stands on the northern shore were very similar to each other, but did not show any particular trend along the length of the transect. Nevertheless, plants of the stable site tended to have both more green and more dry leaves (Fig. 3). The ratio of green to dry leaves had a very similar pattern of spatial distribution at both northern stands, showing a strong relative increase in the number of green leaves in the region of 30 to 70 m of both northern stands (Fig. 3C).

The general appearance of *Phragmites* at the studied stands differed significantly between stands, but the observed and quantified changes of morphological parameters had only one representative, specific direction, as displayed by stem height to diameter ratio (Table 3 and Fig. 3(D)): the taller plants have thicker stems

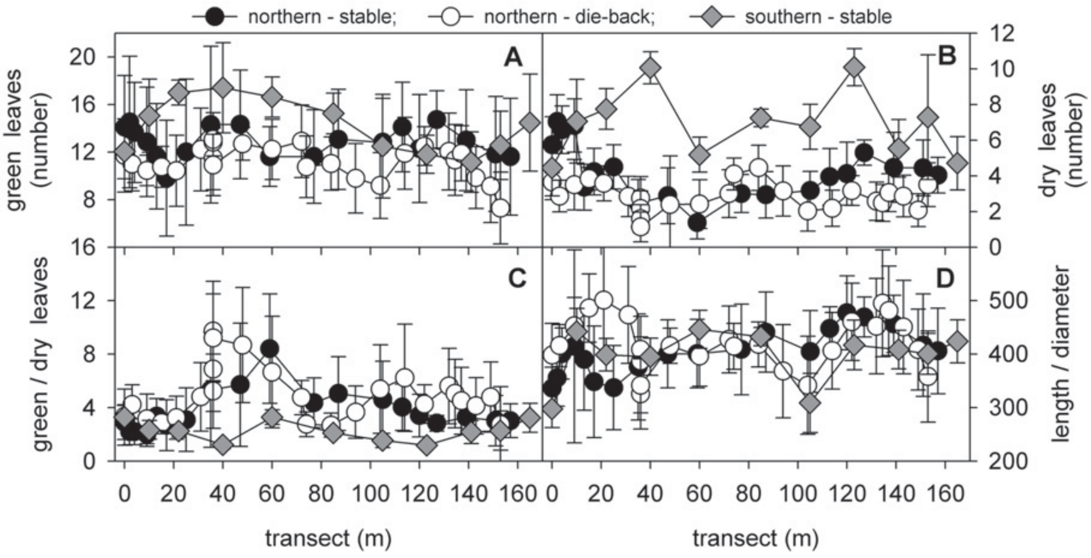

Fig. 3. Changes in morphological parameters of *Phragmites australis* along the stable (black symbols) and die-back (white symbols) stands of the northern shore and stable stands on the southern (grey symbols) shore of Lake Balaton. Each symbol represents average ± SD ($n = 14$–47).

(Tables 3 and 4). Stem height to diameter ratios at similar positions along the transect at each stand were very similar, and showed a relative increase in plants height at 10–30, 50–90 and 110–150 m of each transect (Fig. 3D). However, as the pattern of these changes was very similar for all three stands, there was no statistical difference between the average stem height to diameter ratios of the stands (Table 3).

Plants from the northern stable stand had 88 stems.m^{-2} on average, while the northern die-back and the southern stable stands had lower densities (on average 49 ± 6 and 34 ± 3, respectively) (Table 3). The spatial pattern of reed density change (Fig. 4) provided additional information regarding the difference between the die-back northern and stable southern stands, *i.e.*, the reed density on the southern shore was very homogeneous throughout the whole transect (low variability), whereas density of the die-back stand varied substantially over the length of the transect, between 12 and 142 plants.m^{-2} (Fig. 4). Similar to the northern die-back stand, the stable northern stand displayed significant variability in density along the transect (36–181 stems.m^{-2}), but as density was consistently higher than in the die-back site, the statistical difference between the two stands was significant (Table 3 and Fig. 4).

The following parameters correlated highly ($R > 0.6$) at all studied sites (Table 4):

–plants with more nodes had more green leaves ($R \sim 0.87$),
–taller plants had thicker basal diameter ($R \sim 0.80$), and
–taller stems had more nodes ($R \sim 0.70$).

The height versus diameter and height versus number of nodes parameters displayed a nonlinear (exponential) relationship, while the relationship between number of nodes and number of green leaves was found to be linear

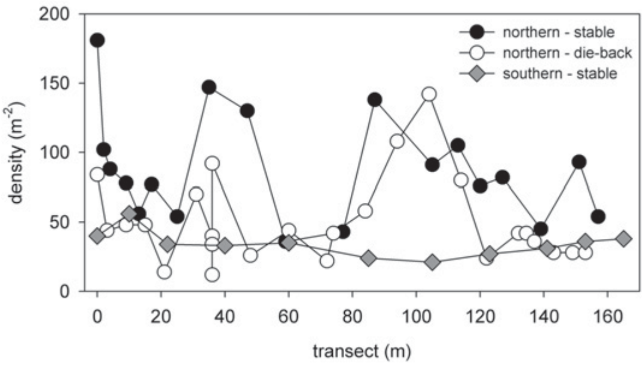

Fig. 4. Changes in *Phragmites australis* stem (green and dry) density along the stable (black symbols) and die-back (white symbols) stands of the northern shore and stable stands on the southern (grey symbols) shore of Lake Balaton.

(data not shown). Other important correlations between the reed morphological parameters can be found in Table 4.

The GLM test showed that the most powerful category influencing the variance of all morphological data of *Phragmites* at the studied sites was the subjective grouping of reed stands by quality (stable versus die-back) (Table 5). The second most influential variable was the difference between individual sites (site-specific difference) that was found to further explain the variance of nearly all the morphometric parameters (Table 5). Whether the stand was located on the northern or southern shore (shore-specific differences) affected the distribution of dry leaf number, internode length, green to dry leaf ratio and number of nodes. Water depth influenced the distribution of the following morphological parameters: green to dry leaf ratio, dry leaf number, stem diameter, number of nodes and height of stems. Spatial position within the

Table 5. Results (F^P) of GLM test of reed morphological parameters as dependent variables. Reed quality (stable or die-back), site (stable northern, die-back northern and stable southern) and shore (northern and southern) as conditional factors, plants as random parameters (data not shown), and position within a transect and water depth as continuous factors. The significance (P) of tests was: ns→$P \geq 0.05$, *→$P < 0.05$, **→$P < 0.01$, ***→$P < 0.001$. For all tests the n is between 132 and 595.

	Quality	Site	Shore	Transect	Water depth
Stem height	518.4***	705.8***	0.4^{ns}	3.2^{ns}	15.7***
Stem diameter	443.4***	703.5***	1.3^{ns}	21.9***	37.2***
Green leaf number	77.8***	57.0***	1.4^{ns}	6.7**	0.1^{ns}
Dry leaf number	70.1***	173.9***	53.1***	12.1***	84.6***
Green/dry leaves	27.6***	69.1***	27.4***	79.0***	143.7***
Node number	152.2***	191.5***	20.3***	0.1^{ns}	21.1***
Internode length	231.8***	356.6***	42.5***	0.7^{ns}	0.8^{ns}
Height/diameter	8.9**	0.8^{ns}	5.1*	14.5***	2.9^{ns}

transect impacted green to dry leaf ratio, stem diameter, height to diameter ratio, dry leaf number and green leaf number (Table 5).

The GLM test also demonstrated that the variance of dry leaf number (and as a result the green to dry leaf ratio) was the most affected of all the tested morphological parameters (Table 5). Stem length to basal diameter ratio was found to be the most stable (least affected) morphological parameter (Table 5), indicating that observed morphologic changes are likely to be unidirectional, *i.e.*, higher plants have thicker basal diameters. The stem length to basal diameter ratio was influenced by plant position within the transect, the reed stand quality (stable versus die-back) and shore-specific variables, but was not influenced by either water depth at the sampling point or the specific properties of the studied sites (Table 5). The GLM results of the stem length to basal diameter ratio suggest what was actually observed: a spatially recurring phenomena at specific water depths at all studied sites (Fig. 3D). This pattern resulted in very similar average data between stands (Table 3) and a strong correlation between stem length and the corresponding diameter (Table 4). The lack of significant, site-specific influence on stem length to basal diameter ratio and similar spatial distribution was also striking (Fig. 3D). The polynomial intra- and extrapolation of the stem length to basal diameter ratios from the stable northern, die-back northern and stable southern stands showed a marked structure within the studied reed stands (Fig. 5).

The phenotypic plasticity of all measured morphological parameters ([max–min]/min) also showed a unique spatial pattern that was very similar along transects of all studied stands (Fig. 5). Phenotypic plasticity peaked at points where the stem length to basal diameter ratio was lowest. Lowest plasticity was observed at spatial positions where the stem length to basal diameter ratio was highest (Fig. 5).

Discussion

Morphological parameters of *Phragmites* in Lake Balaton fit well within the literature of European reed populations (Kühl *et al.*, 1999; Paucá-Cománescu *et al.*, 1999; Hansen *et al.*, 2007), although significant differences were observed between and within the three study sites. In general, the morphological acclimation of *Phragmites* in the northern die-back stand resulted in significantly smaller plants as a result of developmental (lower number of nodes) and growth (shorter internode length) decline. The slowing of plant growth at the die-back site was also manifest in the low number of green leaves (~ 11), and as a result in the low number of dry leaves due to the lack of self-shading. These data fit well with previously published results of *Phragmites* die-back in Lake Balaton (Kovács *et al.*, 1989; Virág, 1997) and in numerous other European lakes (Den Hartog *et al.*, 1989; Ostendorp, 1989; Brix, 1999). These consistent differences between study sites suggest that the morphology of *Phragmites* is influenced not by general, whole-lake-scale factors (climatic, geological, etc.), but depends rather on the unique combination of environmental conditions present at the local, site-specific scale. This could potentially be attributed to nutrient dynamics of the sediment. However, although there was a difference between the sediment composition of the northern and southern stands, none of studied morphological parameters were found to be associated with this. Thus, the possible effect of clone-specific phenotypic variation arises.

Within the sites, there was also a notable spatial pattern of distribution of morphological parameters, particularly of stem length to basal diameter ratios. Both the originally measured (Fig. 3D) and the intra/extrapolated datasets (Fig. 5) show (the latter being more amplified) the three-peak-structure of the real and a hypothetical stand of reed. Due to the similarity of the pattern between stands, it is reasonable to suggest that there are factors beyond clone-specific variability that affect the spatial variation of this morphological parameter within the stands as genetic differences exist between the sites. These must be external, environmental constraints and internal, but extraclonal specificities. Each peak of the spatial distribution of the stem length to basal diameter ratio together with the corresponding minimum of phenotypic plasticity is proposed to correspond to different ecotypes of reed (*i.e.*, a group of clones of *Phragmites* that are adapted to a particular set of environmental conditions). It could be assumed that the

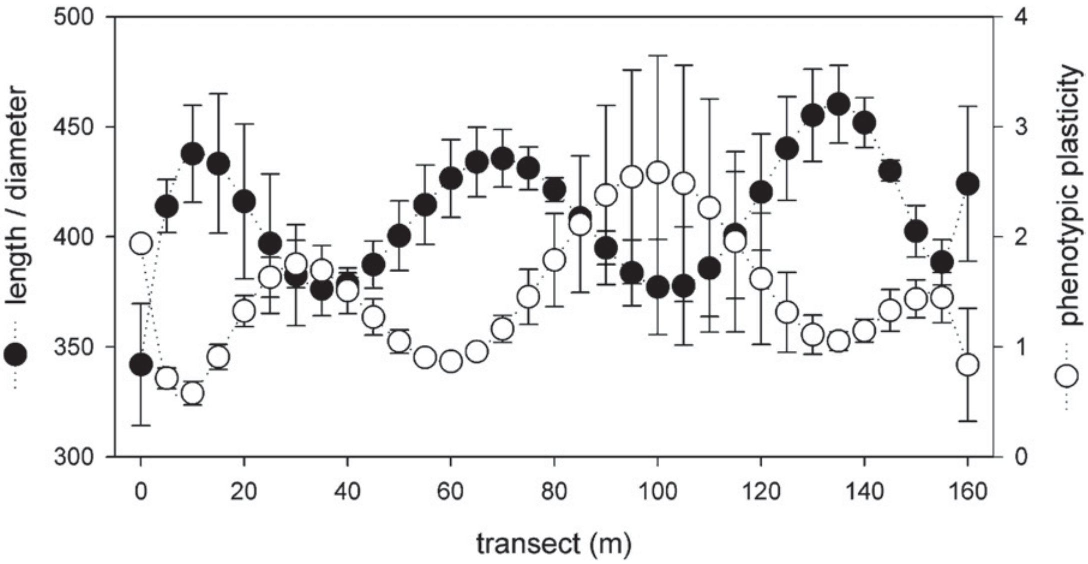

Fig. 5. Change of stem length to basal diameter (cm.cm^{-1}) (black symbols, left *Y*-axis) and phenotypic plasticity ([max–min]/min) (white symbols, right *Y*-axis) of *Phragmites australis* plants from the waterward (0 m) to the terrestrial (155 m) side of a hypothetical transect at Lake Balaton. Each symbol represents average (±SD) of the polynomial extrapolation of the original datasets from the stable northern, die-back northern and southern stands (also see Fig. 3 for "length/diameter").

first peak of the stem length to basal diameter ratio and the associated minimum of the phenotypic plasticity from 0 to 30 m of the transect is related to the deep water ecotype of reed. The reed situated between 40 and 100 m of the transect might correspond to the shallow water ecotype, and the last one (130–150 m) to the flooded terrestrial ecotype of *Phragmites*.

As a result of succession within a reed stand, specific ecotypes of *Phragmites* could evolve at different bathymetric positions, successfully adapting to the particular environment of their growth. Moreover, at the water covered parts of a long-established reed stand where the natural recolonization via seed dispersal is not viable, the most successful clone(s) of *Phragmites* could outgrew others resulting in a dominance of a single genet or a small set of genets (clones) at a given depth (Koppitz, 1999; Engloner *et al.*, 2010; Engloner and Major, 2011). Intraclonal competition of *Phragmites* shoots does not seem to be possible, since there is a physiological integration between ramets (individual plants) of a genet (Pitelka and Ashmun, 1985; Hara *et al.*, 1993; Kroon, 1993). Thus, the possible resource and hormone exchange within the clone maximizes the efficiency of light capture and optimizes the height/diameter versus density relation of the clone for the given habitat, also resulting in a preferential vertical expansion of plants (growth of existing ramets) over horizontal expansion (formation of new ramets) (Kroon, 1993). The physiological integration of a genet influences and maximizes the size of each genet, and organizes the pattern of rhizome branching and shoot dispersion. As a consequence of the regulated rhizome branching and shoot dispersion, a balance between the efficiency of intraclonal cooperation and the being as dense as physiologically possible is maintained to avoid the effect of self-shading, and to prevent invasion by other clones (Pitelka and Ashmun, 1985; Kroon, 1993). In this study, both the standardization of ramet sizes and the uniformization of shoot dispersion were observed in parts of the stands with possibly dominant monoclonal *Phragmites* patches (at transect ranges between 5 and 20, 60 and 80, 120 and 150 m of transects).

At transitional parts of the transect (at stem length to basal diameter ratios minima and corresponding peaks of phenotypic plasticity), between 20 and 60 and 80 and 120 m, the abiotic factors are adequate for all neighbouring ecotypes. In these regions, competition between clones leads to cessation of vertical growth and favours the increase in number of different genets. The high density of genets leads to increased interclonal competition and consequently to a local increase of plant density, lowering the stem/diameter ratio as was described previously for other clonal plants (Pitelka and Ashmun, 1985; Kroon, 1993). The height difference between neighbouring genets affects the light conditions that benefits the clone and leads to asymmetric competition, as in non-clonal plant populations (Weiner and Solbrig, 1984; Hara, 1994; de Kroons and Hutchings, 1995). At multiclonal parts of the stands, this competition also leads to a significant increase in the phenotypic plasticity of *Phragmites*.

This also demonstrates the possibility to distinguish between the *Phragmites* ecotypes on the basis of morphological parameters, however, genetic evidence is also needed. Nevertheless, the striking similarity of the pattern of spatial distribution of some morphologic parameters, in particular, the stem length to basal diameter ratio of *Phragmites*, observed at very different sites shows that in reed the main source of phenotypic variation is the abiotic specificity of the stand rather than the genetic component. The similar pattern of spatial distribution of this ratio could follow the bathymetric constrains of each ecotypes.

We could assume that the deep water ecotype of *Phragmites* in Lake Balaton dominates the part of the stands with water higher than 35 cm, while the shallow water and terrestrial ecotypes of reed are concentrated at parts of stands with little (~ 5 cm) or no standing water over the sediment, respectively. Moreover, in terms of methodology this strong zonation of reed stands may jeopardise conventional discrete sampling techniques, increasing the importance of understanding internal stand structure.

Morphological and physiological adaptation of plants to water depth results in zonation within wetlands (Hutchinson, 1975; Vretare *et al.*, 2001; Bailey-Serres and Voesenek, 2008). A large number of studies reflect that in multispecies wetlands resources competition between the species results in zonation and also triggers species succession (Wilson and Keddy, 1986; Wetzel and van der Valk, 1998; Keddy, 2005), but relatively little is known about competition within monospecific wetlands. Furthermore, there is no data at all on how intraclonal cooperation might affect boundaries and zonation of *Phragmites*. The results of the present study suggest that at sites with no nutrient limitations it is water depth that limits the distribution of *Phragmites* morphotypes.

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