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The phenotypic plasticity of *Glyceria fluitans* growing over the water/land gradient

Fenotipska plastičnost vrste *Glyceria fluitans* na prehodu voda/kopno

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Abstract. The amphibious species *Glyceria fluitans* successfully thrives in an intermittent ecosystem Lake Cerknica, where floods alternate with dry periods. The species grows over the environmental gradient from open water to dry land. The plant's phenotypic plasticity was studied analysing anatomical, morphological, biochemical and physiological characteristics in specimens from different locations. Floating leaves were thicker, having abundant aerenchyma, lower chlorophyll a+b contents and higher chlorophyll a/b ratio. The relative amounts of total UV-B and UV-A screening compounds per leaf area were high and similar in all forms that indicated possibly saturated amounts. The measurement of fluorescence parameters revealed no disturbance in energy harvesting since the values of potential and effective photochemical efficiencies, photochemical and non-photochemical quenching were similar over the gradient.

Key words: *Glyceria fluitans*, land/water gradient, amphibious character

Izvleček. Amfibijska vrsta *Glyceria fluitans* se pojavlja v presihajočem ekosistemu Cerkniškega jezera, kjer se poplave izmenjujejo s sušnimi obdobji. Vrsta porašča širok pas na prehodu iz vode na kopno. Na podlagi nekaterih anatomskih, morfoloških, biokemijskih in fizioloških analiz rastlin na prehodu smo ugotavljali fenotipsko plastičnost vrste. Plavajoči listi so bili debelejši, z obsežnejšim aerenhimom, nižjo vsebnostjo klorofila a+b in višjim razmerjem med klorofiloma a in b. Relativna vsebnost UV-B in UV-A zaščitnih snovi na listno površino se med proučevanimi oblikami ni bistveno razlikovala kar kaže na saturirane vrednosti. Izmerjeni parametri fluorescence so odražali nemoten privzem energije, saj so bile vrednosti potencialne in dejanske fotokemične učinkovitosti ter fotokemičnega in nefotokemičnega dušenja podobne na celotnem prehodu iz vode na kopno.

Ključne besede: Glyceria fluitans, prehod med kopnim in vodo, amfibijske značilnosti

Introduction

Macrophytes are limited to the macroscopic flora including aquatic spermatophytes, pteridophytes and bryophytes. Their growth form usually classifies them in four-group system, which is widely accepted: emergent macrophytes (i.e. *Phragmites australis*), floating-leaved macrophytes (i.e. Nuphar luteum), free-floating macrophytes (i.e. *Eichhornia crassipes*) and submerged macrophytes (i.e. *Myriophyllum spicatum*). Some plants are not restricted to one category only due to their amphibious character (Fox 1992). Plants/species with an amphibious character plants are found among all major groups of plants, including mosses, ferns and angiosperms (Hutchinson 1975).

In the intermittent water bodies, such as Lake Cerknica, water depth and water retention play a major role in the occurrence of plant species (Fernández-Aláez & al. 1999). The water level raising drowns emergent plants, while lowering exposes submerged ones to drying, freezing or heat (Cronk & Fennessy 2001). Plants/species with an amphibious character plants possess either distinct aerial and aquatic leaves (heterophylly) either different shoots or growth forms (Hutchinson 1975, Fox 1992). The phenotypic plasticity enables the species to colonize a range of habitats. It is an expression of flexibility in evolutionary strategy of the species (Menadue & Crowden 1990).

Amphibious character gives them the ability to photosynthesize under contrasting conditions in aquatic and terrestrial environment (Germ 2002). Beside morphological adaptations, amphibious plant species may also respond to the fluctuations of water by changing the reproduction strategy (Boulton & Broc 2001).

Scarce information on *Glyceria fluitans* is available in the literature (Jogan 1996). We hypothesised that the species possessing temporal or spatial segregated submerged, floating and emergent shoots might have a competitive advantage over less tolerant submerged or emergent macrophytes in habitats characterised by water fluctuations, such as Lake Cerknica. To get an insight into survival strategy of *G. fluitans*, growing over environmental gradient in an intermittent Lake Cerknica, we studied some anatomical, morphological, biochemical and physiological characteristics. The latter included the measurements of fluorescence parameters that give us useful information about the ability of plants to tolerate the water level fluctuations.

Materials and methods

Area description

The study was carried out in Lake Cerknica (45°45'N, 14°20'E) during extremely dry vegetation season in June 2003. The closed depression of Cerkniško polje extends on an area of 38 km^2 and usually the area of 25 km^2 is flooded when the polje changes into a lake. The Lake Cerknica is locus typicus for intermittent lakes and karst poljes. The water reaches its normal level of 550 m a.s.l. in spring and late autumn to early winter (Kranjc 2002a, Kranjc 2002b). Usually in summers the lake becomes dry.

Material studied

Glyceria fluitans L. belongs to Poaceae family (Martinčič & al. 1999). It colonizes more or less permanent, shallow still or slowly running water. It is widespread to scattered in lowland and lower montane area rarely exceeding 600 m a.s.l. (Jogan 1996). We examined different growth forms of *G. fluitans* growing over environmental gradient from open water to dry land (1 – open water; 2 – water-land interface, 3 – 2 m from water body, 4 – dry land).

Morphological and anatomical analyses

In samples collected at different locations we measured the total stem length and counted the number of leaves per stem. We determined the thickness of leaves, spongy tissue and palisade tissue and calculated the palisade/spongy tissue ratio. Dry weights were obtained after drying the plant material at 105°C for 24 hours.

Biochemical analyses

For determination of chlorophylls (chl a+b and chl a/b ratio) we followed the equations developed by JEFFREY & HUMPHREY (1975). The chlorophyll extracts were made using 90% (v/v) acetone solution. The chlorophyll contents were calculated considering absorption values at 647, 664 and 750 nm measured with UV/VIS Spectrometer System (Lambda 12, Perkin-Elmer, Norwalk, CT, USA). The extracts of UV-A and UV-B screening compounds we made using the methanol solution Šmethanol : distilled water : HCl (37% (v/v)) = 79:20:1Ć. We followed the method proposed by CALDWELL (1968). The extinctions of the samples were measured in the UV-B spectral range 280-320 nm and UV-A spectral range 320-400 nm (Lambda 12, Perkin-Elmer, Norwalk, CT, USA). The extinctions were integrated for UV-A and UV-B range and expressed in relative units per dry mass and per area.

Measurements of fluorescence parameters

Measurements of chlorophyll a fluorescence were carried out on clear days during dry period in summer 2003. Photosynthetic photon flux density (PPFD) was more than 1100 mmol/m2s, relative humidity around 40% and temperature (air and water) was in range between 20°C and 25°C. The measurements of chlorophyll fluorescence were made using a modulated fluorometer (OS-500 fluorometer; OPTI-SCIENCES, Tyngsboro, MA, USA). The actual (yield) and potential (Fv/Fm) photochemical efficiencies were measured to estimate the disturbance to light harvesting in different plant forms from different locations. Values of Fv/Fm were obtained after dark-adaptation by using dark-leaf clips for 10 minutes. Fv stands for variable fluorescence. This is the difference between maximal (Fm) and minimal (Fo) fluorescence in dark-adapted leaves excited with a saturating beam of white light. The yield of illuminated sample was defined as (F´m-F´o)/F´m (F´m is maximal and F´o is minimal fluorescence of light-adapted leaves) (CAMPBELL & al. 2003). The photochemical (qP) and non-photochemical (qN) quenching was traced using a series of saturating pulses of white light (PPFD=8000 mmol/m2s; 0.8s). Sample leaves for kinetics determination were dark adapted for 30 minutes.

Statistical analysis

The measurements were carried out on 5 parallel samples. Standard deviations (SD) were calculated. The analysis of variance (one factor ANOVA) was performed to estimate the differences among locations over environmental gradient.

Results and discussion

The intermittent Lake Cerknica is characterised by extreme water level fluctuations. The flora of Cerkniško polje is very diverse, due to great diversity of biotopes and specific water regime (MARTINČIČ 2002). The life histories of plants in the lake are intimately coupled to the periodicity of the water regime (GABERŠČIK & al. 2004). The water level fluctuations are a limiting factor for the

plant growth, development and reproduction (GABERŠČIK & URBANC-BERČIČ 2002); therefore the growth of plants/species with an amphibious character is favoured (GABERŠČIK & MARTINČIČ 1992, MARTINČIČ 2002, MARTINČIČ & LESKOVAR 2002).

G. fluitans thrives at the locations were the water is present also in dry period. At that time this species occupies the locations from open water to dry land, exhibiting different growth forms in contrasting environment. The analysis of the habitus of plants revealed that plants in open water developed more leaves than terrestrial ones, but the length of the plants was the highest in both extreme locations. The leaves became thinner with the increasing distance from the water body, due to less developed spongy tissue (Tab. 1). Looser tissue, well developed in floating specimens, might improve the floating ability of leaves. Abundant aerenchyma contributes to lower specific leaf weight of floating leaves, even though they are much thicker. Thicker floating leaves were also found in a case of *Polygonum amphibium* (GABERŠČIK & MARTINČIČ 1992). *P. amphibium* exhibited only slight differences in palisade/spongy tissue ratio. It seems that thicker floating leaves are an attribute of many plants/species with an amphibious character (HUTCHINSON 1975, NIELSEN 1993). On a contrary, the floating leaves in *Batrachium peltatum* were thinner than aerial ones (NIELSEN & SAND-JENSEN 1993).

Tab. 1. Morphological, anatomical and biochemical characteristics of *Glyceria fluitans* growing over the environmental gradient (1 - open water; 2 - water-land interface, 3 - 2 m from water body, 4 - dry land) in Lake Cerknica.
Tab. 1. Morfološke, anatomske in biokemijske značilnosti vrste *Glyceria fluitans* rastoče v različni oddaljenosti od proste vodne površine (1 - odprta vodna površina, 2 - prehod med vodo in kopnim, 3 - 2 m od vodnega telesa, 4 - kopno) na Cerkniškem jezeru.

Characteristic	Location			
	1	2	3	4
Total steam length [cm]	89 ± 7	48 ± 3	66 ± 4	87 ± 10
No. leaves per steam	7.8 ± 0.4	6. 7 ± 0.5	6.6 ± 0.9	4.9 ± 0.9
Leaf thickness [µm]	539 ± 120	372 ± 74	256 ± 38	180 ± 22
Palisade/spongy tissue	0.28 ± 0.08	0.44 ± 0.06	0.80 ± 0.22	2.15 ± 0.47
Spec. leaf weight [g/dm^2]	33.8 ± 6.9	35.2 ± 9.0	39.1 ± 2.8	40.7 ± 1.6
Spec. leaf area [dm^2/g]	0.031 ± 0.008	0.028 ± 0.001	0.025 ± 0.002	0.024 ± 0.001
Chl *a+b* [mg/gDM]	7.19 ± 1.34	14.87 ± 2.45	10.05 ± 2.09	8.49 ± 2.17
Chl *a/b*	7.19 ± 2.95	3.95 ± 0.31	3.90 ± 0.48	5.35 ± 3.17

Amphibious species exhibit great variability in chlorophyll content (GERM & GABERŠČIK 2003). The floating leaves of *G. fluitans* had lower chlorophyll a+b content (mg g-1 dry mass) than the emergent leaves (Tab. 1). The investigations of *Callitriche copocharpa* and *Batrachium peltatum* are in line with our results (NIELSEN 1993, NIELSEN & SAND-JENSEN 1993), but this was not the case in *Batrachium aquatile* (NIELSEN 1993). We determined the highest values of chlorophyll a/b ratio in floating leaves. This might be a consequence of the fact that a lot floating leaves were more exposed to irradiation, while aerial leaves were erect and therefore they avoided high irradiance flux during midday.

The ability of plants to protect themselves from UV radiation plays the important role in open habitats. The majority of primary producers is able to produce UV screening compounds that present an UV-B selective filter (BJÖRN 1999). This appears to be an important protective mechanism because they could effectively reduce detrimental effect of UV-B radiation in leaves (MIDDELTON & TERAMURA 1993). In *G. fluitans* the relative amount of total UV-B and UV-A screening compounds per unit of dry mass (Fig. 1)

was the highest in floating leaves. The investigations reveal that UV absorbing compounds are mainly synthesised in epidermis of the leaves that prevent UV penetration into the mesophyll (Day & al. 1996). For that reason we also compared the amounts of total UV-B and UV-A screening compounds per unit of leaf area. The values showed no significant difference among different forms. These results are in agreement with other researches of plants/species with an amphibious character (Germ & al. 2002). The comparison of the amounts determined in *G. fluitans* with other amphibious and terrestrial plants revealed relatively high values in the former. That indicated possibly saturated amounts of UV-B and UV-A screening compounds. The production is probably genetically fixed and less dependent on environmental factors. A similar phenomenon was found in *Potamogeton nodosus* (Les & Sheridan 1990).

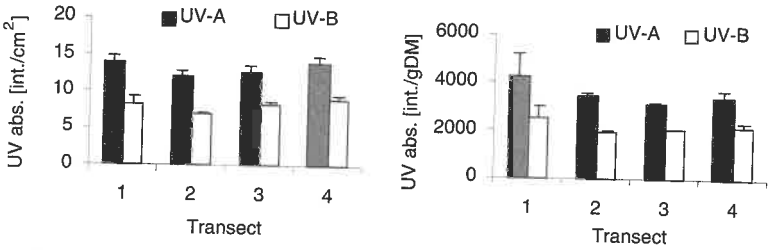


Fig. 1. The amount of UV absorbing compounds of *Glyceria fluitans* growing over the environmental gradient (1 - open water; 2 - water-land interface, 3 - 2 m from water body, 4 - dry land) in Lake Cerknica.
Sl. 1: Količina UV absorbirajočih snovi pri vrsti *Glyceria fluitans* rastoče v različni oddaljenosti od proste vodne površine (1 - odprta vodna površina, 2 - prehod med vodo in kopnim, 3 - 2 m od vodnega telesa, 4 - kopno) na Cerkniškem jezeru.

The water-logging should not cause a physiological stress in macrophytes, although photochemical efficiency might be disturbed due to other stresses which are the consequence of water level fluctuation; i.e. drought (Colom & Vazana 2003), photoinhibition (Gaberščik & Mazej 1995, Ralph & Burchett 1995, Beer & Björk 2000, Mouget & Tremblin 2002, Campbell & al. 2003) and UV-B radiation (Conde-Alvarez 2002, Gaberščik & al. 2002, Germ et al. 2002). Our results showed no significant differences in potential (Fv/Fm) and actual (yield) photochemical efficiencies of PS II in *G. fluitans* growing over the environmental gradient (Fig. 2, Tab. 2). Fv/Fm was close to the opti-

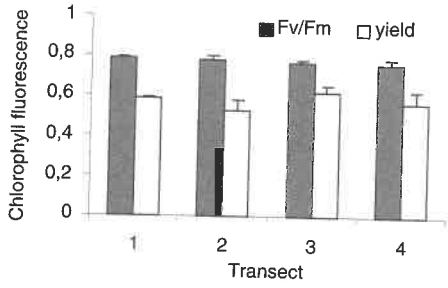
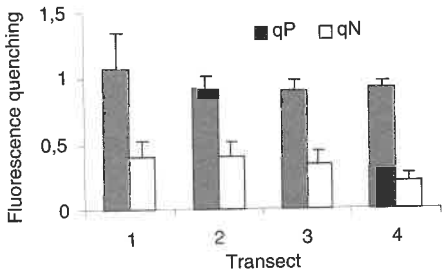


Fig. 2. Photochemical efficiency of *Glyceria fluitans* growing over the environmental gradient (1 - open water; 2 - water-land interface, 3 - 2 m from water body, 4 - dry land) in Lake Cerknica.
Sl. 2: Fotokemična učinkovitost vrste *Glyceria fluitans* rastoče v različni oddaljenosti od proste vodne površine (1 - odprta vodna površina, 2 - prehod med vodo in kopnim, 3 - 2 m od vodnega telesa, 4 - kopno) na Cerkniškem jezeru.

mal values (0.83) at all locations as an indication of normal function of PS II. Lower values of yield indicated the presence of stress with no respect to the location and form. WALDHOFF & al. (2002) also found no correlation between the changing water levels and the Fv/Fm ratios of the tree species *Symmeria paniculata.* The leaves fully retained the potential to photosynthesize during the aerial and aquatic phases. Fv/Fm ratio in *Genipe americana* also remains constant despite flooding conditions (MIELKE & al. 2003). Our study revealed no differences in photochemical (qP) and nonphotochemical (qN) quenching in *G. fluitans* appearing in different growth forms over the gradient water-land (Fig. 3). Photochemical quenching had greater values and affected the actual photochemical efficiency more than non-photochemical quenching. Values of qN in *Genipe americana* increase by flooding, while qP remains constant (MIELKE & al. 2003).

Fig. 3. Photochemical and non-photochemical fluorescence quenching in *Glyceria fluitans* growing over the environmental gradient (1 - open water; 2 - water-land interface, 3 - 2 m from water body, 4 - dry land) in Lake Cerknica.
Sl. 3. Fotokemično in nefotokemično dušenje fluorescence pri vrsti *Glyceria fluitans* rastoče v različni oddaljenosti od proste vodne površine (1 - odprta vodna površina, 2 - prehod med vodo in kopnim, 3 - 2 m od vodnega telesa, 4 - kopno) na Cerkniškem jezeru.



Tab. 2. The significance of differences of investigated plant characteristics among 4 locations over environmental gradient water/land (ANOVA) (1 - open water; 2 - water-land interface, 3 - 2 m from water body, 4 - dry land) in Lake Cerknica.
Tab. 2. Statistična značilnost razlik pri proučevanih značilnostih rastline med 4 lokacijami na okoljskem gradientu voda/kopno (ANOVA) (1 - vodno telo, 2 - prehod med vodo in kopnim, 3 - 2 m od vodnega telesa, 4 - kopno) na Cerkniškem jezeru.

Characteristic	Significance	Characteristic	Significance
Total steam length [cm]	***	UV-A [int./gDM]	NS
No. leaves per steam	***	UV-B [int./gDM]	*
Leaf thickness [μm]	***	UV-A [int./cm^2]	NS
Palisade/spongy tissue	***	UV-B [int./cm^2]	**
Spec. leaf weight [g/dm^2]	*	Fv/Fm	NS
Spec. leaf area [dm^2/g]	NS	Yield	*
Chl *a+b* [mg/gDM]	***	Photchemical quenching	***
Chl *a/b*	NS	Non-photchemical quenching	***

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; non significant (NS) $p > 0.05$.

Conclusions

The floating shoots of *G. fluitans* develop thicker leaves than emergent ones. They have abundant aerenchyma that contributes to lower specific leaf weight and their floating ability.

The floating leaves had higher chlorophyll a/b ratio than the emergent ones, which might be due to higher irradiance of direct sunrays. The relative amount of total UV-B and UV-A screening compounds showed no significant difference among diverse forms of *G. fluitans*.

No significant differences in potential and effective photochemical efficiencies as well as in photochemical and non-photochemical quenching were found over the environmental gradient. These fluorescence characteristics indicate normal functioning of PS II.

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Povzetek

Glyceria fluitans je vrsta z amfibijskim značajem in raste v presihajočem ekosistemu Cerkniškega jezera, ki ga označujejo izmenjave poplav in sušnih obdobij. V sušnem delu leta, ko nivo vodne gladine upade, porašča širok pas na prehodu iz vode na kopno. *G. fluitans* v odvisnosti od vodnih razmer, ki so pogojene prostorsko ali časovno, tvori morfološko različe poganjke. V vodi razvije poganjke, ki so potopljeni ali plavajoči, na kopnem pa zračne poganjke. V raziskavi smo ugotavljali fenotipsko plastičnost vrste na prehodu iz vode na kopno. Spremljali smo nekatere anatomske, morfološke, biokemijske in fiziološke parametre posameznega tipa poganjkov. V naravnem okolju smo s pomočjo parametrov fluorescence ugotavljali uspešnost prestrezanja energije. Rezultati so pokazali, da so plavajoči listi *G. fluitans* debelejši, z obsežnejšim aerenhimom, ki zmanjšuje specifično listno težo in prispeva k večji plovnosti. Nižja vsebnost klorofila a+b in višje razmerje med klorofiloma a in b pri plavajočih listih pa sta odraz večje jakosti sevanja zaradi direktnih sončnih žarkov. Realtivna vsebnost UV-B in UV-A zaščitnih snovi na listno površino je bila v vseh proučevanih oblikah podobna in je nakazovala saturirane vrednosti. Izmerjeni parametri fluorescence klorofila a v FS II so odražali normalno fotosintezno aktivnost vrste na celotnem prehodu iz vode na kopno. Vrednosti potencialne fotokemične učinkovitosti (Fv/Fm) so bile na celotnem prehodu blizu optimalni vrednosti 0,83. Dejanska fotokemična učinkovitost (yield) je bila nižja od potencialne, kar je rezultat rahlega stresa, vendar pa razlik na gradientu nismo opazili. Tudi vrednosti fotokemičnega in nefotokemičnega dušenja so bile podobne na celotnem prehodu iz vode na kopno.

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