Why do aquatic carnivorous plants prefer growing in dystrophic waters?

Zakaj vodne karnivore rastline rastejo v distrofnih vodah?

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Abstract: The majority of aquatic carnivorous plants (ACPS; *Aldrovanda, Utricularia*) usually grow in shallow dystrophic waters. In these habitats, rootless ACPs usually grow together with rooted aquatic non-carnivorous plants (N-ACPs). Yet species diversity of rooted N-ACPs in dystrophic lakes is relatively poorer than that of abundant ACPs. If generally true, why do rootless ACPs prefer growing in shallow dystrophic waters and why is the occurrence of rooted N-ACPs in these waters limited? These questions are elucidated on the basis of different specific adaptive traits of both functional groups and a different treatment of external habitat factors on both plant groups.

Keywords: aquatic carnivorous plants, *Aldrovanda, Utricularia,* submerged rooted plants, free CO_2, humic acids, pH, potential species pool, water dystrophy

Izvleček: Večina vodnih karnivorih rastlin (VKR; *Aldrovanda, Utricularia*) navadno uspeva v plitvih, distrofnih vodah. V takšnih habitatih, VKR brez korenin rastejo skupaj z ukoreninjenimi ne karnivorimi vrstami (N-VKR). Vrstna pestrost ukoreninjenih N-VKR v distrofnih jezerih je manjša kot pestrost množično zastopanik VKR. Če je to res, zakaj VKR brez korenin rastejo vplitvih distrofnih vodah in zakaj je pojavljanje ukoreninjenih N-VKR omejeno? Odgovori na ti dve vprašanji sta podani na osnovi potez prilagajanja obeh funkcionalnih skupin in različnim obravnavanjem obeh skupin rastlin z zunanjimi habitatnimi parametri.

Ključne besede: vodne karnivore rastline, *Aldrovanda, Utricularia,* potopljene ukoreninjene rastline, prosti CO_2, huminske kisline, pH, potencialna prisotnost vrst, distrofna voda

Introduction

The functional group of aquatic carnivorous plants (ACPs) comprises the species *Aldrovanda vesiculosa* L. (Droseraceae) and about 50 species of the genus *Utricularia* L. (Lentibulariaceae) (Taylor 1989, Adamec 1997, 2011, Guisande et al. 2007). The majority of these plants usually

grow in shallow dystrophic (humic) waters and most of them are considered rare and strongly or critically threatened (Casper and Krausch 1981, Murphy 2002). In their recent minireview, Ellison and Adamec (2011) have thoroughly compared ecophysiological traits and cost-benefit trade-off of rooted terrestrial and rootless aquatic

carnivorous plants. They have concluded that the ecophysiological differences between these functional groups within carnivorous plants are greater than those between ACPs and rooted submerged aquatic non-carnivorous plants (N-ACPs) and also between terrestrial carnivorous and non-carnivorous plants. In their shallow dystrophic habitats, rootless ACPs usually grow together with rooted N-ACPs. Yet, on the basis of literature (e.g. Kamiński 1987, Murphy 2002), Ellison and Adamec (2011) have stated that species diversity of rooted N-ACPs in dystrophic lakes is relatively poorer than that of abundant ACPs. If generally true, why do rootless ACPs prefer growing in shallow dystrophic waters and, in contrast, why is the occurrence of rooted N-ACPs in these waters limited? Furthermore, are these reasons based more on different specific adaptive traits of both functional groups or on a different treatment of external (unfavourable) ecological habitat factors on both plant groups?

The characterization of dystrophic waters

Dystrophic or humic waters are usually characterized primarily by increased concentration of humic acids (+ tannins), causing the water to have a brownish colour, and by lower pH values (Hansen 1962). However, such a characterization is quantitatively rather vague as there are many types of dystrophic waters (e.g. peat bogs, fen lakes, forest pools, reed-dominated lake littorals). These types differ greatly from each other in the organic sediment composition, dominant vegetation and, also, water chemistry. Generally, it is difficult to determine where dystrophy starts. It is thus reasonable to differentiate the degree of dystrophy (*sensu* Chmiel 2010). The other associated symptoms commonly occurring in dystrophic waters are low electric conductivity (i.e. soft waters) and low concentration of mineral forms of N and P (sometimes also K^+) within the range of oligo-mesotrophy (Kamiński 1987, Adamec 2007, 2008, Guisande et al. 2007); this results in the waters exhibiting low biological productivity. Due to slow decomposition of loose organic sediment (composed of mosses, reed or sedge litter), the usually low concentration of dissolved

oxygen in dystrophic waters is accompanied by high concentration of free CO_2 (Adamec 1997, 2007). Summarily, the unfavourable factors affecting rooted submerged vascular vegetation are high concentration of humic acids and tannins, dark water associated with very steep temperature gradient (overheating at the surface, cold at the bottom) and considerable light attenuation and shift of light spectrum in deeper water, low pH values, hypoxia in the free water column and anoxia in the partly decomposed, loose organic bottom sediment (litter), which is unsuitable as a rooting medium for rooted submerged plants. The only advantage (high $[CO_2]$) cannot evidently prevail over the unfavourable factors (Adamec 1997, 2007, 2008, Murphy 2002). As an exact definition of dystrophic waters is difficult for the above hydrochemical reasons, the opposite phytosociological approach considering the typical dystrophic vegetation may be used for denoting dystrophic waters (Murphy 2002). An analysis of the main water chemistry factors, using both published and unpublished data for 307 microsites of 11 ACP species on four continents, shows clearly that the amplitudes of all estimated parameters are extremely broad (Fig. 1). Yet the means, medians and quartiles for all parameters characterize truly the essence of shallow dystrophic waters. Fifty % of the waters have high $[CO_2]$ within 0.14–0.92 mM.

The ecophysiological characterization of aquatic carnivorous plants

ACPs are always rootless and float freely below the water surface or are weakly attached to loose sediments, submerged or even amphibious. Most ACPs have a linear and modular shoot structure consisting of nodes with filamentous leaves and tubular internodes. The majority of species have homogeneous green shoots bearing traps. Several species have dimorphic shoots differentiated into green photosynthetic and pale carnivorous (trapping) ones attached to sediments (Taylor 1989). Moreover, ACPs show very rapid apical shoot growth of 1.0–4.2 nodes d^{-1} (see Adamec 2011) but their basal shoot segments die at about the same rate ("conveyer-belt" growth system); the new biomass is allocated into branching and flowering only. Thus, due to the special growth form and the
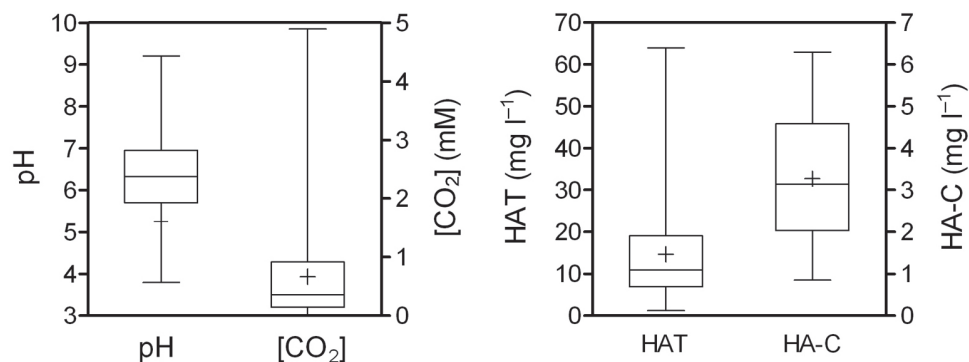
Figure 1: Analysis of main water chemistry factors at world sites of aquatic carnivorous plants from literature data and unpublished results (n = 34–307). Boxes show median (central horizontal line), upper and lower quartiles (limits of boxes), and range of values (horizontal bars delimiting vertical lines). Asterisks show mean. Mean pH was calculated via [H$^+$]. HAT, sum of humic acids and tannins; HA-C, carbon of humic acids.

Slika 1:   Analiza glavnih parametrov kemizma vode na različnjih svetovih rastiščih karnivorih rastlin (podatki iz literature in neobjavljeni podatki; n = 34–307). Srednja črta v škatli je mediana, zgornja in spodnja meja 1. in 2. kvartil in ročaji 3. in 4. kvaril. Zvezdice označujejo srednjo vrednost. Srednji pH smo izračunali na podlagi [H$^+$]. HAT, vsota huminskih kislin in taninov; HA-C, ogljik v huminskih kislinah.

absence of roots, photosynthetic shoots of ACPs can always float at or near the water surface at a relatively high irradiance even in frequently oscillating water levels, while rooted N-ACPs with slower apical growth are firmly anchored in the bottom growing in the deep shade. If ACP species with dimorphic shoots are attached to the bottom by their pale carnivorous shoots, due to shoot plasticity and rapid apical growth, their photosynthetic shoots can reach the water surface faster (Adamec 2007). In spite of possible generative reproduction of most ACPs (Taylor 1989), this way is probably limited mostly to colonisation of new sites and/or restoration of sites after drying out. Most ACP species propagate at their sites mainly vegetatively by shoot branching and separation of branches (Kamiński 1987, Adamec, 2011). Numerous European N-ACP species of the genera *Potamogeton*, *Callitriche* and *Ranunculus* regularly set larger and germinating seeds and their proportion of vegetative propagation may be obviously much lower. As seed germination in dystrophic habitats occurs under unfavourable conditions (for small seedlings) of hypoxia/anoxia, deep shade and low temperature at the bottom, the generative recovery of both functional plant groups is greatly impaired. Yet rootless ACP seed-

lings sprout at the water surface under favourable conditions – this difference could also favour the occurrence of ACPs. Similarly, most temperate ACPs form turions (overwintering buds) which usually overwinter at the bottom of water bodies but germinate and sprout at the water surface under favourable conditions again, while the not-so-common turions of N-ACPs (*Potamogeton* spp.) are either permanently attached to the bottom or exclusively sprout there (Adamec 2010). So, this adaptive trait of ACPs also supports their growth in dystrophic waters.

Under favourable conditions, ACPs exhibit very rapid growth: the relative growth rate ranges between 0.035–0.15 d^{-1} (Adamec 2011, Ellison and Adamec 2011). Frequent shoot branching is a symptom of such a rapid growth. The rapid growth of rootless ACPs in nutrient-poor dystrophic waters requires several ecophysiological adaptations: high photosynthetic rate, prey capture, efficient nutrient re-utilization from senescent shoots and high nutrient uptake affinity from the ambient water (Adamec 2011). All ACP species are strict CO_2 users and their high net photosynthetic rates at [CO_2] >0.2 mM are among the highest values found in N-ACPs (Adamec 1997, 2011). Thus, high [CO_2] occurring at most sites of ACP

(usually >0.1 mM; Fig. 1) together with a medium irradiance at the water surface (>*c.* 100 µmol m^{-2} s^{-1} PAR) are the first prerequisites for attaining high photosynthetic rates and, consequently, high growth rates. Based on only several ACP species, it is evident that N and P are re-utilized from aged shoots very efficiently but all K$^+$ is lost (Adamec 2011). Similar information is lacking for N-ACPs. Prey capture in rootless ACPs in dystrophic waters can cover even a considerable proportion of their seasonal N and P gain, giving them definite advantage over rooted N-ACPs, but many nutrient-poor dystrophic waters exhibit very low prey availability minimising this advantage (Richards 2001, Adamec 2008, 2011, Peroutka et al. 2008). It is therefore possible to assume that ACP shoots have a very high uptake affinity for mineral nutrients from the ambient water.

The potential occurrence of ACPs and N-APCs in dystrophic waters

The comparison of data on the relative abundance of both functional plant groups from the literature and unpublished data from110 microsites in six Central European countries (Poland, Slovakia, Czech Republic, Germany, Switzerland, NE France with ACPs (mostly *Aldrovanda, U. vulgaris, U. australis*) was performed (Table 1). The potential community species pool at these sites comprised seven ACPs (all Central European species, i.e., *A. vesiculosa* +6 *Utricularia* species, cf. Casper and Krausch 1981) and 44–52 vascular lowland submerged N-ACP species (depending on the country; Casper and Krausch 1981) mostly of the genera *Potamogeton, Ranunculus, Callitriche, Myriophyllum* (including rootless *Ceratophyllum* spp. and amphibious *Pilularia globulifera, Hottonia palustris, Luronium natans, Eleocharis acicularis, Juncus bulbosus, Sparganium natans* and floating-leaved *Potamogeton natans,* but excluding montane *Isoëtes* spp., *Ranunculus fluitans* growing strictly in streams and partly emergent *Stratiotes aloides*), which are usually rooted and have the dominant part of submerged plant biomass. Although the mean species number of N-ACPs (2.12 ± 0.26) was significantly greater (*t* test; *P* < 0.05) than that of ACPs (1.49 ± 0.07), the relative diversity of N-ACPs expressed in %

of the potential species pool (4.24 ± 0.51) was highly significantly lower (*P* < 0.0001) than that of ACPs (21.3 ± 1.0). Although this approach is rather simplified and biased and one can discuss what is the real potential species pool of submerged plants in dystrophic waters in each country and at each site studied, the analysis shows clearly that the relative diversity of N-ACPs is limited. Only 24 species of N-ACPs out of the potential species pool were found at these sites. Moreover, the most common co-occurring N-ACP species were *Potamogeton natans, Juncus bulbosus* and *Lemna trisulca* which are not strictly submerged. *P. natans* has a good deal of natant foliage, *J. bulbosus* is ecologically an extremely plastic amphibious species and *L. trisulca* is an amphibious non-rooting species. It is also possible to assume that N-ACPs tend to grow rather in waters at a lower degree of dystrophy. However, due to unsufficient data, this cannot be proven. Comparing the occurrence of both functional groups in dystrophic waters, different phylogenetic constraints should be mentioned for both groups of plants. All ACPs, except for the monotypic genus *Aldrovanda*, are all confined to sections of the single genus *Utricularia* (Taylor 1989) and, thus, must be highly phylogenetically constrained; this fact suggests their relatively good adaptation to growing in dystrophic waters. On the contrary, submerged N-ACPs are phylogenetically (and also ecologically) a very diverse group (see e.g. Casper and Krausch 1981) and consist of subgroups such as rooted in the bottom, rootless, amphibious, rooted with partly floating leaves. The great diversity of N-ACPs predetermines also a diversity of the degree of their adaptations to shallow dystrophic waters.

Generally, these data support the above view that rooting in the bottom is not beneficial for submerged plants in dystrophic waters and that the prevailing strategy of aquatic plants in these waters is to reach or follow the (oscillating) water surface. The question raised above may be answered in that specific adaptive traits of ACPs (no roots, rapid apical growth, turions, high photosynthetic rate, high nutrient uptake affinity, carnivory) mitigate the impact of some unfavourable ecological factors of dystrophic waters (anoxic organic bottom, dark water, low nutrient concentration) on ACPs when compared with N-ACPs. The unfavourable water chemistry factors (humic acids and tannins,

Table 1: Analysis of the occurrence of aquatic carnivorous plants (ACPs) and aquatic submerged non-carnivorous vascular plants (N-ACPs, usually rooted species) at sites of ACPs in six Central European countries from literature data and unpublished results (n = 110). Potential community species pool is expressed in % as the proportion of each functional group to the potential maximal species number (7 for ACPs; 44–52 for N-ACPs).

Tabela 1: Analiza pojavljanja vodnih karnivorih rastlin (VKR) in vodnih ne-karnivorih rastlin (N-VKR, navadno neukoreninjenih) na mestih z VKR v šestih srednje evropskih državah na podlagi literaturnih in neobjavljenih podatkov (n = 110). Potencialna zastopanost vrst v združbi je izražena v % kot delež vsake funkcionalne skupine glede na potencialno maksimalno število vrst (7 za VKR; 44–52 za N-VKR).

Plant group	Species number Mean ± SE	Potential species pool (%)		
		Mean ± SE	Median	Quartiles
ACPs	1.49 ± 0.07	21.3 ± 1.0	14.3	14.3; 28.6
N-ACPs	2.12 ± 0.26	4.24 ± 0.51	2.27	0.0; 6.0

low pH) affect both functional plant groups in the same way but ACPs seem better adapted to tolerate these factors.

To understand better the specific adaptive traits of ACPs for growing in dystrophic waters, ACP tolerance of high concentrations of humic acids and tannins (excessive to most N-ACPs) should preferentially be studied as the key factor. Are they essential for ACP growth? What are their concentration limits for single species? Are humic acids able to cover a part of seasonal N gain? Our knowledge of this subject is still very fragmentary (see Kamiński 1987). Another mystery associated with mineral nutrition of ACPs is K^+ economy. Dystrophic waters are commonly very poor in K^+ but shoot K content in ACPs is relatively high (median 1.6% dry weight; Ellison and Adamec 2011). Moreover, animal prey is considered a rather poor K^+ source and, thus, the total K^+ uptake from prey is very limited (Adamec 2011). However, zero re-utilization of K^+ from senescent shoots was reported in two ACP species (Adamec 2011). Do these facts indicate a very high K^+ uptake affinity of ACP shoots from the ambient water? Traps of many aquatic *Utricularia* species live close to great amounts of organic detritus (Adamec 2007) which is frequently aspirated into the traps. How important can the utilisation of organic detritus for the seasonal N, P and K gain in aquatic *Utricularia* species in dystrophic waters be?

Conclusions

The ability of ACPs to easily follow the favourable water surface conditions both during the growing season and after overwintering together with their carnivory confers a great ecological advantage over rooted N-ACPs when growing in dark dystrophic waters. The great potential of high [CO_2] occurring in these waters can be fully exploited. Thus, the ecological cost/benefit relationships for growing in shallow dystrophic waters are much more optimised in ACPs than rooted N-ACPs. The possibility of capturing animal prey together with high CO_2 availability were obviously the key favourable ecological factors which "drove" the adaptive evolution of ACP ancestors to living in dystrophic waters.

Acknowledgements

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