

MORPHOMETRY OF SHOOTS AND FLOWERS OF *UTRICULARIA MINOR*
AT A LARGE SITE IN THE CZECH REPUBLIC

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Abstract: In 2021, a large population of *Utricularia minor* was found in a revitalized former sand-pit with strongly acidic and dystrophic water in the Czech Republic. The plants in the population were robust, highly branched, flowered prolifically, and set seeds. The mean length of main shoots of robust *U. minor* plants was 72 cm (range 54-90 cm). Each plant had a total of 7-17 branches. Inflorescences with at least one ripening fertile capsule were 11-33 cm long and bore 6-11 flowers or capsules at different ages. However, only two ripe fertile capsules (mean 1.21) formed at maximum in one inflorescence.

Introduction

Utricularia minor L. (lesser bladderwort) is a temperate perennial aquatic carnivorous plant with a circumboreal distribution in Eurasia and North America but also extending to Papua New Guinea (Casper 1974; Taylor 1989). *Utricularia minor* usually has monomorphic (non-differentiated) shoots 5-30 cm long that bear both filamentous or flattened photosynthetic “leaves” in regular leaf nodes and 1-2.5 mm long carnivorous traps (Taylor 1989; Fleischmann & Schlauer 2014). However, based on ecological conditions (mainly water depth or terrestrial growth), the size and morphology of the shoots are enormously variable: from a very slender thread-like habit on emergent wet soils to more robust, frequently branched habit as a submerged plant; yet partly differentiated shoots into green photosynthetic and pale carnivorous bearing the majority of traps are rather rare. Due to the ability of *U. minor* to grow both submerged and emerged, it can be considered fully amphibious. During the warmest season, the plants form an erect raceme inflorescence 3-25 cm long emerging from the water and bearing 2-6 light-yellow flowers (Casper 1974; Taylor 1989; Fleischmann & Schlauer 2014). Flowers can form ripe globose capsules 2-3 mm in diameter with several seeds.

In Europe, *U. minor* grows with a highly scattered distribution in bogs, fens, peaty fishponds, peaty meadows, backwater pools, springs, and also in shallow sand-pits. It usually grows in very shallow water 2-20 cm deep and often semi-terrestrially. The plants growing in very shallow water are usually loosely anchored in the bottom, while those growing in deeper water (>30 cm) are mostly floating freely at the surface. As opposed to the very similar but more stenotopic *U. bremii*, *U. minor* as a eurytopic species grows in a great variety of waters: within the pH from 3.5 to 9.2, in very soft to medium hard waters and in clear to strongly dystrophic (humic), dark-brown waters (Adamec 2020); *U. bremii* within the pH from ca. 5.0 to 7.5. It usually grows together with other

Utricularia species: *U. australis*, *U. intermedia*, *U. ochroleuca*, and/or *U. stygia*. In the Czech Republic, it is declared a vulnerable species (VU) of the Czech flora (Grulich 2017) with ca. 50 sites mostly in S, N, and E Bohemia (Adamec, unpubl. data), but it is not a legally protected species. In spite of the relatively high number of Czech sites, the majority of them are small, extending only several m² and consisting of a few hundreds of individuals.

Relatively very few detailed data on the morphology, growth traits, reproduction, and ecology or physiology of *U. minor* are available (see Taylor 1989; Hofmann 2001; Navrátilová & Navrátil 2005a,b; Peroutka *et al.* 2008; Fleischmann & Schlauer 2014; Adamec 2020). However, pollen morphology of *U. minor* has been described in detail (Casper & Manitz 1975; Beretta *et al.* 2014). According to both studies, the species does not form malformed pollen though ripe fertile capsules are formed only in a small proportion of flowers (Adamec, unpubl. data).

In this paper, we present morphometric investigations of shoots and inflorescences of *U. minor*, with an emphasis on shoot branching traits, formation of fertile capsules and seed set, in a numerous population of the species in a revitalized former sand-pit in the Czech Republic, and ecological requirements of *U. minor* are discussed.

Site description

Robust plants of *U. minor* were investigated in a newly revitalized, old sand-pit near Hrdlořezy in the Třeboňsko Biosphere Reserve and Protected Landscape Area in S Bohemia, Czech Republic (48.86393°N, 14.82833°E; Fig. 1). The shallow sand-pit is about 170 years old, its water depth is 20-100 cm, consists of several closely adjacent water bodies and has a total area of ca. 0.3 ha. It is closely surrounded by a Scots pine (*Pinus sylvestris*) forest growing on the wet, strongly acidic soils which causes the water in the sand-pit pools to be strongly humic.

In the autumn 2020, the *Sphagnum* carpet and organic sediments in the large southern pool were excavated stepwise to the sandy bed to the depth of 30-65 cm and the organic sediment was removed. In the 2021 growing season, *U. minor* has spread into the southern excavated pool and, due to optimal conditions, has formed a dense prolifically flowering stand with a total coverage of 60-100% in the whole pool (Fig. 1).

In the dark-brown water of the pool, robust flowering *U. minor* plants were growing near the surface in the open-water zone or were weakly anchored in floating “islands” of brown filamentous peat, which were released from the bottom after the pool excavation (Fig. 2). The *U. minor* stands represented the early successional stage of the vegetation of oligotrophic, humic water bodies, close to the vegetation of Sphagno-Utricularion alliance with scattered aquatic *Carex rostrata* plants and two submerged acidophilous species of *Sphagnum* mosses (*S. fallax*, *S. cuspidatum*). Sparsely distributed plants of both *U. minor* and *U. australis* occurred



Figure 1: Southern humic pool in a forest sand-pit near Hrdlořezy, S Bohemia, Czech Rep., inhabited by a dense stand of flowering *U. minor*, 23 July 2021.



Figure 2: Left: Detailed view on peaty floating islands with a dense stand of *U. minor*. Water depth is 30-60 cm. Right: Flowers of *U. minor*. Note relatively narrow corolla with enrolled margins.

also in the former *Equiseto fluviatilis*-*Caricetum rostratae* stands (Magno-Caricion elatae alliance, Šumberová *et al.* 2011) in an original, non-revitalized part of the sand-pit in some smaller pools dominated by aquatic *C. rostrata* and *Sphagnum* stands and by *Juncus effusus* on the shores.

Methods

On 23 July 2021, we isolated 10 large *U. minor* plants and measured the length of the shoots using a plastic ruler. Very carefully, we isolated another 14 large plant individuals from the open-water zone in order to estimate the detailed shoot structure with an emphasis on branching traits (after Adamec 2011a): total main shoot length in terms of the number of mature leaf nodes, number of 1st- and 2nd-order branches and their length in term of the number of mature leaf nodes, number of internodes between two successive branches in main shoots and branches, number of inflorescences, and the dry weight (DW, 80°C). As the plants were strongly entangled with each other, it was very difficult to separate quite intact plant individuals. Thus, most plants were slightly damaged and the estimated values can be considered partly conservative. Some plants were flowering. The collected plants were transported in water in a bucket to the laboratory for processing. Using a battery-powered conductometer, electrical conductivity was measured in two different parts of the



Figure 3: Left: Ripe capsules of *U. minor* from the sand-pit pool near Hrdlořezy. Ripe seeds are visible through the wall of the capsules. Right: Abortive, sterile capsules of *U. minor*. Note the small size and pale colour. Ticks indicate 1 mm.

southern pool with the dense *U. minor* stand and in other three smaller pools inhabited scarcely with *U. minor* and *U. australis* and water samples were collected for measuring pH in the laboratory. Due to very low pH, the measured conductivity was corrected for the measured pH (subtraction of 3.25 mS/m for the pH of 4.00 and/or 100 $\mu\text{M H}^+$; Sjörs 1952).

On 4 August 2021, 14 *U. minor* plants with at least two inflorescences each were carefully separated and the internodes on the main shoot between two inflorescences were counted. Fourteen robust inflorescences each bearing at least one big ripening capsule (Fig. 3) were collected together with a part of the main shoot. In a closed vessel, they were transported to the laboratory. The length of inflorescences, number of all flowers (capsules) or developing flower buds and number of ripening fertile capsules were estimated. Capsules were scored as fertile if they were relatively big (ca. 3 mm; cf. Fig. 3). They were formed mainly in the basal part of the inflorescences; the others were considered sterile. For full ripening of the capsules and seeds, the inflorescences were then put in a closed 1 L mini-aquarium containing ca. 300 mL of dystrophic water with a bit of peat. The mini-aquarium floated in water in a big plastic outdoor container for another month and all fertile capsules could fully ripen and set seeds. The number of ripe seeds (Fig. 4) per capsule was estimated.

As the experimental plants had different numbers of branches, means of 14 individual plants were averaged. When possible, means \pm SE intervals and ranges for individual plants are shown. The significant difference between comparable values was tested using the Student's t-test. The aim of the study was also to estimate what is the interrelationship of the apical shoot growth rate (ASGR, expressed as the number of newly formed leaf nodes per day) of main shoots and branches (see Adamec 1999, 2011a). As new branches are initiated on the apex of the main shoot, they grow together with the main shoot. When the number of mature leaf nodes from the apex is estimated in main shoots and long branches in a population of plants then the linear regression of these couples of data determines both the position of the main shoot, where theoretically the zero mature leaf node is formed, and the ratio between the ASGRs of main shoots and branches. The advantage of this analysis is based on no need of estimation of ASGR alone.

Results and discussion

The mean length of main shoots of robust *U. minor* plants was 71.6 \pm 3.8 cm (range 54-90 cm) though only 30 cm has been stated in the literature (e.g., Casper 1974; Taylor 1989). In other plants, main shoots consisted on average of 61 mature leaf nodes (range 48-83, Table 1). The robust and frequently flowering plants had on average 8.7 \pm 0.50 1st-order branches, while had only 2.0 \pm 0.73 2nd-order branches and together a total of 7-17 branches. Main shoots branched on average relatively regularly after each 12.2 \pm 0.92 leaf nodes, while branches did more irregularly only after 16.8 \pm 4.1 leaf nodes – these values were not significantly different from each other ($P>0.05$). Branching in

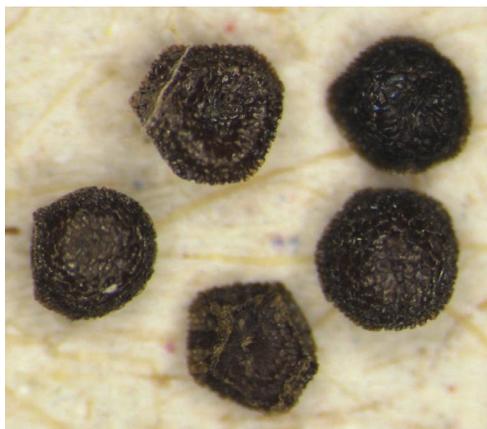


Figure 4: Ripe seeds of *U. minor*. The seed diameter is ca. 0.55 mm.

Table 1. Morphometric characteristics of robust *Utricularia minor* plants in a dense stand in a dystrophic sand-pit near Hrdlořezy, S Bohemia, Czech Republic; DW, dry weight. Means \pm SE intervals based on averages for individual plants are shown, n=14. Range of values shown for individual plants.

Parameter	Main shoot length (nodes)	Number of branches per plant			Internodes between two branches		Plant DW (mg)
		1 st order	2 nd order	All	Main shoots	Branches	
Mean	60.7	8.7	2.0	10.7	12.2	16.8	37.7
SE	2.7	0.50	0.73	0.73	0.92	4.1	5.1
Range	48-83	6-13	0-9	7-17	3-30	7-41	22.3-96.5

robust (and frequently flowering) *U. minor* plants is thus similar to that in *U. australis* and photosynthetic shoots of *U. stygia* and *U. intermedia* (branching after each 5.9-22.6 leaf nodes; for the review, see Adamec 2018). In *U. minor* plants with two or more flowers, subsequent flowers occurred on average after each 10.1 ± 0.49 (median 10; range 6-13) leaf nodes of the main shoot. However, this value was not significantly different from the branching of the main shoot. Mean DW of *U. minor* plants was only 37.7 ± 5.1 mg and flowering plants had the highest DW values (Table 1). The DW values of robust *U. minor* plants are about 10-13 times lower than those of robust *U. australis* plants, but quite the same as those for *U. australis* plants from a very oligotrophic site (Adamec 2011). Therefore, even a very dense stand of robust *U. minor* possessing a slender habit can produce about one order of magnitude lower biomass than a dense stand of *U. australis*.

The linear regression of the number of leaf nodes of main shoots and branches revealed a highly significant correlation according to the linear equation:

$$\text{Nodes of branches} = 0.833 \times \text{Nodes of main shoots} - 7.46 \quad (n=25; r=0.937; P<0.0001).$$

Thus, on average, main shoots started forming the first branches with mature leaf nodes and traps between the 7th to 8th mature leaf nodes as counted from the apex. Mean ASGR of branches reached only 83% of that of the main shoots. This value obviously reflects the strength of apical dominance of the main shoot apex as a sink for mineral and organic nutrients and is in line with the values found in *U. australis* (about 85% at an optimal and 65% at a barren site; Adamec 2011a) and in younger branches of *Aldrovanda vesiculosa* (67%; Adamec 1999). To the best of our knowledge, the ASGR of *U. minor* has never been measured. However, in the very similar *U. breinii* in a growth experiment, fed plants formed 2.4 new leaf nodes a day (Adamec 2011b). Assuming this ASGR also in *U. minor* and mean branching after each 12.2 leaf nodes (Table 1), a new branch could be initiated on the main shoot every ca. 5.1 days. Exactly the same branching frequency of 4.7-5.5 days was found for field-grown *U. australis* and *A. vesiculosa* (Adamec 2018). Thus, *U. minor* has a similar relative growth rate as reported for other temperate aquatic *Utricularia* species (see Adamec 2018).

Selected inflorescences with at least one ripening fertile capsule were 11.4-33.3 cm long and bore 6-11 flowers or capsules at different stages of development (Table 2, Fig. 5). However, only two ripening fertile capsules (mean 1.21) formed at maximum in one inflorescence. Single flowers formed acropetally, i.e., from the base to the apex – similarly as in other aquatic *Utricularia* species (Taylor 1989). Although small, non-opened flower buds were usually initiated at the apex of the sampled inflorescences at the time of sampling (Fig. 5), these apical flower buds occasionally

Table 2. Characteristics of ripe inflorescences of *Utricularia minor* plants. Means \pm SE intervals based on averages for individual plants are shown, n=14. Range of values shown for individual plants.

Parameter	Inflorescence length (cm)	Number of flowers	Fertile capsules	Seeds per capsule (n=32)
Mean	15.7	8.5	1.21	2.66
SE	0.83	0.36	0.32	0.30
Range	11.4-33.3	6-11	1-2	1-7

opened fully in the mini-aquarium in the next weeks but, together with small capsules, they never formed fertile capsules. Ripe capsules with red spots are circumscissile (Figs. 3, 5) but they usually do not open and seeds are released only after the capsules have rotted. Ripe capsules contained on average only 2.66 ± 0.30 ripe seeds (median 2; quartiles 1 and 3; range 1-7) but each capsule always contained several abortive seeds. Dark-brown ripe seeds of a discoid shape were ca. 0.55-0.60 mm large (Fig. 4; cf. Taylor 1989), while abortive seeds were of irregular prismatic shape or very thin (i.e., without endosperm). The mean weight of one ripe seed (as based on the weight of 20 seeds) was 78.9 μ g and this value was exactly the same as that of *U. vulgaris* seed (L. Adamec, unpubl. data). If *U. minor* forms normal functional pollen in open flowers (Casper & Manitz 1975; Beretta *et al.* 2014) but only a small proportion of flowers form fertile capsules and set seeds, it may indi-



Figure 5: Ripening inflorescences of *U. minor* each with utmost two fertile capsules. Ticks indicate 1 mm.

cate that pollination is the limiting process for seed set in this species. Production of ripe seeds in flowering *U. minor* populations leads to formation of a seed bank but the production of ripe seeds within a population may not be high. However, the ecological regulation of seed germination and seed longevity are unknown.

In the newly revitalized southern pool of the sand-pit with the robust flowering *U. minor* plants, pH of the humic water was within 4.15-4.35 and was within 4.14-4.67 in other smaller pools inhabited loosely with *U. minor*. The bicarbonate concentration was thus zero and the concentration of free CO₂ could not be calculated from carbonate equilibria but probably was >0.1 mM. In line with the very low pH and absence of bicarbonate, electrical conductivity corrected for the pH in the southern pool was only 0.10-0.85 mS/m and 0.69-0.98 mS/m in the other pools. Such low conductivity values support the view that the water was very nutrient-poor. In sampled robust *U. minor* plants, >50% of mature traps contained either captured animal prey or dense suspended particles of dark-brown humic acids. In the water, low abundance of small crustacean zooplankton species from the families Daphnidae and Cyclopidae were found. Evidently, *U. minor* plants gain a dominant part of mineral nutrients N and P for their growth from zooplankton or humic acids (cf. Adamec 2018). As this pool is surrounded by a dense Scots pine forest, it is possible that also Scots pine pollen grains are randomly captured by *U. minor* traps and utilized as prey (Peroutka *et al.* 2008). Growing in dark-brown humic water, the robust flowering *U. minor* plants were only distributed within the surface water layer of 1-5 cm deep or were attached on the top of floating peaty islands (Fig. 2). Moreover, as the whole southern pool was almost unshaded by the ambient forest, the plants were growing at full irradiance and in a surface layer of warm water. The subsurface water layer is very beneficial for the growth of *U. minor* in deeper water bodies. This ecological benefit may not apply to semiterrestrial microhabitats where the attached plants can either dry out or be flooded during frequent water level fluctuations.

In conclusion, morphometric and growth traits have been specified in robust flowering plants of *U. minor* in a strongly acidic, humic forest sand-pit. Evidently, the size of robust plants and inflorescences is much larger than published in the 'classic' literature. As the principal ecological factors enabling the robust plant habit and prolific flowering, the following items have been suggested: high CO₂ concentration, frequent capture of prey and/or humic acids by traps, high irradiance, and warm water. This study has confirmed the eurytopic character of *U. minor* insofar as strongly acidic, well-lit, dark-brown waters represent one of several ecological optima of this species. Another optimum can be in very shallow, clear, and neutral or slightly alkaline waters.

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