

COMPARATIVE SHOOT MORPHOLOGY BETWEEN
CULTIVATED *UTRICULARIA BREMII* PLANTS AND THOSE GROWING IN
NATURAL HABITATS IN THE CZECH REPUBLIC

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Abstract: In summer 2023, the morphometry of large adult plants of *Utricularia bremii* was studied in an outdoor culture and at three shallow pools in two oligotrophic sand-pits in South Bohemia, Czech Republic, with a focus on shoot length and biomass, shoot branching traits and ecological conditions. Overall, the mean length of main shoots was 34-43 cm (range 23-73 cm) and the shoots bore on average 11-18 branches of three orders. On main shoots, branches were initiated on average every 7.7-9.2 internodes, which indicates a very fast propagation and growth. A new branch is theoretically initiated every ca. 3.3-3.8 days. This study confirms that shallow, well-lit, oligomesotrophic, soft-water sand-pit pools may represent an ecological optimum for this species.

Introduction

Utricularia bremii Heer ex Kolliker is a temperate perennial aquatic carnivorous plant with a distribution in Central, Western, Northern and North-Eastern Europe (Casper 1974; Taylor 1989; Fleischmann & Schlauer 2014; Adamec 2020). It has usually monomorphic (non-differentiated) shoots up to 50-60 cm long (but commonly only 20-30 cm) that bear both filamentous or flattened photosynthetic “leaves” in regular leaf nodes and 1-2.8 mm long traps (Fig. 1). Rarely, the shoots are partly differentiated into green photosynthetic ones with a lesser number of traps, and paler carnivorous ones with many traps and leaf filaments immersing into a soft substrate (Taylor 1989; Fleischmann & Schlauer 2014; Adamec 2020). Nevertheless, quite similarly as in a ‘twin’ species, *U. minor* (Adamec & Kučerová 2022), the size and morphology of the shoots are enormously variable: a very slender thread-like habit occurring on emergent, wet sandy barren soils may be changed to more robust, frequently branched habit when growing submerged in more trophic waters. Therefore, the habit of *U. bremii* markedly depends on ecological conditions (mainly water depth or terrestrial growth or trophic level) and the species can be considered fully amphibious. During June to August, the plants form an erect raceme inflorescence 5-50 cm long emerging from the water and bearing 2-14 light-yellow flowers (Taylor 1989; Fleischmann & Schlauer 2014; Adamec 2020). However, inflorescences only ca. 10-25 cm high were observed repeatedly at several Czech sites where the plants prolifically flower (L. Adamec, pers. observ.). In spite of spectacular yellow flowers (Fig. 2), the plants are usually sterile due to pollen malformation and do not set seeds (Casper & Manitz 1975; Taylor 1989; Beretta *et al.* 2014). The shape of corolla is basically the only determination mark between *U. bremii* and *U. minor* (Fleischmann & Schlauer 2014; Adamec 2020). As observed at South Bohemian sites in the Czech Republic repeatedly, flowering of *U. bremii* requires

longer periods of warm summer weather, shallow water (1-5 cm) with stable level (L. Adamec, pers. observ.) – the same requirements which allow flowering of similarly rare European *Utricularia* species (see Adamec 2020).

Utricularia bremii grows with a highly scattered distribution in peatbogs, fens, peaty fishponds, peaty meadows, backwater pools, springs, and also in small 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 substrate, while those growing in deeper water (>25 cm) are mostly floating freely at the surface. As opposed to the very similar and much more common and eurytopic *U. minor*, *U. bremii* as a partly stenotopic species grows within the narrow pH from ca. 5.0 mesotrophic waters (for the review, see Adamec 2020), while *U. minor* within the wide pH from 3.9 to 7.5 in very soft to slightly hard waters and in clear to strongly dystrophic (humic), brownish, oligo- to 9.2. At the reported *U. bremii* sites, electrical conductivity ranged from 1.2-42.4 mS/m, total alkalinity from 0.11-0.46 meq/L, free CO₂ concentration from 0.11-0.34 mM, NH₄⁺-N from 0.2-41 µg/L, PO₄-P from 1.9-25 µg/L and NO₃⁻-N was 0.0 µg/L. However, as the reported sites were mainly soft-water sand-pits, it is possible to consider that the ecological amplitude of *U. bremii* is much wider. *Utricularia bremii* usually grows together with *U. australis* (Adamec 2020). In the Czech Republic, it is declared a critically endangered species (C1) of the Czech flora (Grulich 2017) with ca. 10 natural sites mostly in W, S and N Bohemia (Adamec 2020) and is a legally protected species. Between 2008-2012, local *U. bremii* has been introduced to five oligotrophic shallow sand-pits in the Třeboň basin, S Bohemia, Czech Republic, where large populations have arisen since (Adamec 2020). As judged to several Czech sites, both species-poor, very shallow (0.5-5 cm) microhabitats in

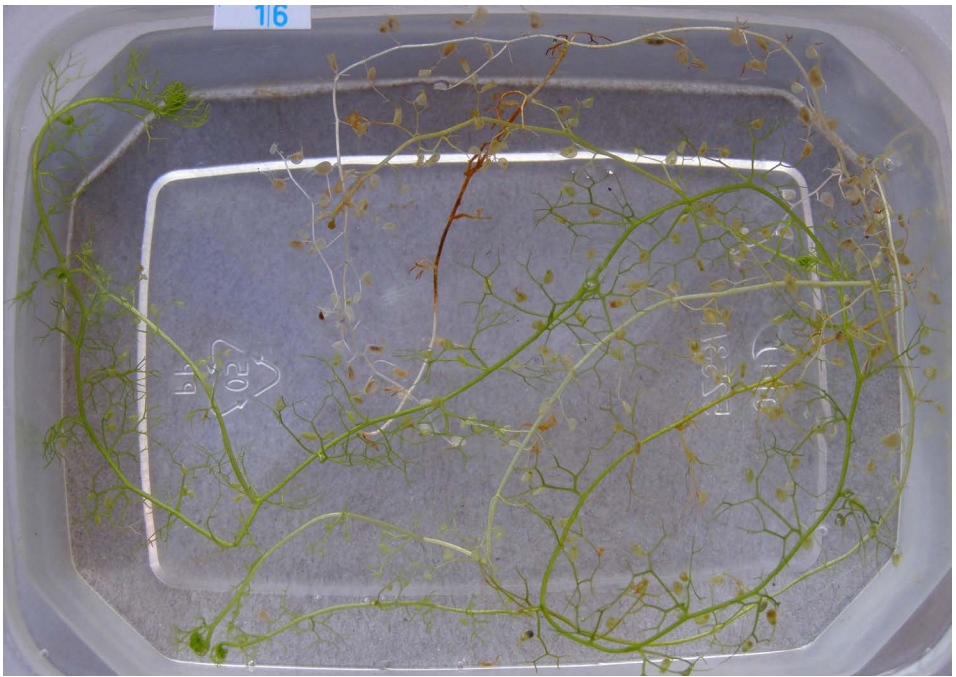


Figure 1: Detailed view on a robust, markedly branched plant of *U. bremii* collected from the Suchdol Southern pool. Note partly decaying basal leaf nodes stained by ferric precipitates. The white bar indicates 1 cm.

well-lit shallow sand-pit pools without water level fluctuations and shaded dystrophic forest pools may represent an ecological optimum for this species, which is characterized by high cover and stand biomass and prolific flowering (Adamec 2020).

As opposed to *U. australis* and *U. vulgaris*, which maintain more or less constant shoot length at maturity during a great deal of the growing season ('conveyer-belt' system of shoot growth; Adamec 2018), *U. bremii* (and also *U. minor*) rather increase gradually their mother shoot length up to the initial stage of autumnal turion formation (Adamec 2020). Afterwards, the mother shoots are gradually shortened up to the turion length due to the decay of senescent basal shoot segments. Owing to the rarity of *U. bremii*, very few detailed data on its morphometry, growth traits, and eco-physiology are known (see Taylor 1989; Fleischmann & Schlauer 2014; Adamec 2018, 2020). The rapid vegetative growth of *U. bremii* includes both rapid apical shoot growth of mother shoots and high branching rate (Adamec 2011, 2018, 2020). The mean apical shoot growth rate of 2.40 ± 0.14 leaf nodes day^{-1} was found in a greenhouse-growth experiment in *U. bremii* shoot segments fed on prey, while non-fed control plants formed only 1.30 ± 0.15 nodes day^{-1} and 3.3 times less branched (Adamec 2011). Moreover, fed plants branched after each ca. 12 leaf nodes on the main shoot ('branching rate') and/or each 5.0 days ('branching frequency'). Feeding on prey in *U. bremii* is thus just as important for supporting the growth as in other aquatic carnivorous plants (cf. Adamec 2018, 2020).

Here, I present morphometric investigations of robust *U. bremii* shoots in its dense stands at three microsites at two artificial sites in shallow oligo-mesotrophic, former sand-pits in the Czech Republic, and in an outdoor culture in the Institute of Botany at Třeboň, Czech Republic. An



Figure 2: Detail of a typically flat and wide corolla of *U. bremii* from the Suchdol sand-pit.

emphasis is put on shoot length and biomass, shoot branching traits, and ecological conditions. This study tightly follows up on a recent paper by Adamec & Kučerová (2022) conducted on *U. minor* in the same region and allows to better compare both species.

Site description

Plants of *U. breinii* were investigated in an 80 cm deep, 2 m² outdoor plastic container in the collection of aquatic and wetland plants in the Institute of Botany, Czech Academy of Sciences, at Třeboň, Czech Republic, in two small shallow pools (denoted as Southern and Northern) in a former sand-pit near Suchdol nad Lužnicí, and in a shallow pool in an old sand-pit near Cep. All these sites lie in the Třeboňsko Biosphere Reserve and Protected Landscape Area in S Bohemia, Czech Republic (ca. 49°N, 15°E, elevation 430-445 m a.s.l.).

The outdoor container in the collection was kept as a ‘moderately dystrophic pool’ with slightly brownish water and a variety of submerged and emergent plants. The container was shaded by a green plastic gardener’s net and the PAR irradiance at the surface was reduced to ca. 30-40% of that in the open. A dense stand of *U. breinii* was distributed from the surface up to the depth of ca. 25 cm. Plant dominants in the container were *Carex limosa*, *Eriophorum angustifolium*, *Comarum palustre*, and *Nymphaea candida*. Medium-hard tap water was used to cover water losses.

In the Cep sand-pit, rather slender *U. breinii* plants were collected in a large shallow pool (ca. 0.1 ha) from a dense stand around 2 m from the shore at a water depth of 20-25 cm (Fig. 3).



Figure 3: Shallow shore of the Cep sand-pit with dominant but slender *U. breinii*.

Juncus bulbosus, *J. effusus*, *Eleocharis acicularis*, *Glyceria fluitans*, *Utricularia australis*, *Peplis portula*, and a submerged acidophilous *Sphagnum cuspidatum* were the local dominant plants growing in full sunlight. A clayish-organic light sediment 2-3 cm deep occurred on the bottom.

In the Suchdol sand-pit, *U. bremii* plants were collected from two small adjacent pools ca. 15 m² large which were only 3 m away from each other, i.e., the Southern and Northern pool. The Southern pool (Fig. 4) was 10-25 cm deep (the water level in both pools was lower by 6 cm at the time of sampling than the normal one is) and *U. bremii* plants here were more robust than in the Northern pool. The Northern pool (Fig. 5) was 10-20 cm deep. A clayish-organic sediment ca. 10 cm deep lay on the bottom in both pools. It was covered by loose, brown-red ferric precipitates of Fe(OH)₃ to which *U. bremii* shoots were immersed (Fig. 6). Plant dominants in both pools were *U. australis*, *Alisma plantago-aquatica*, *Typha latifolia*, and *Juncus effusus* on the shores. Pools in both sand-pits were supplied mainly with rain water and, therefore, they contained very soft water.

Methods

The sampling of *U. bremii* plants from all four microsites was conducted between 29 July and 2 August 2023 when long shoots reached around their maximal lengths and started decaying at their bases (Fig. 1) where senescent turion leaves were usually present. At each of the four microsites, 14 large intact plants were very carefully separated from neighboring plants, deprived of sessile organisms and washed gently in the pool water. An emphasis was put to that each sampled plant was as long, branched and intact as possible. The very fine shoots were



Figure 4: The shallow Southern pool in the Suchdol sand-pit with robust *U. bremii*.



Figure 5: The very shallow and densely overgrown Northern pool in the Suchdol sand-pit.

rather entangled with each other and it was very difficult to separate quite intact plant individuals. Several plants were slightly damaged and, thus, the estimated values have to be considered slightly conservatively. The collected plants did not flower. Each wet plant was put into a plastic bag without water and carefully transported to the laboratory for processing. At each microsite, electrical conductivity was measured using a pocket conductometer and water samples were collected for estimation of pH and total alkalinity in the laboratory as well as for mineral nutrient analyses. Free CO_2 concentration was calculated from pH and total alkalinity (for all analyses, see Adamec 2009).

The detailed shoot structure was estimated in all plants (Adamec & Kučerová 2022): total main shoot length in terms of cm and the number of mature leaf nodes, number of 1st- and 2nd- plus 3rd- order branches and their lengths in terms of the number of mature leaf nodes, number of internodes between two successive branches in main shoots and branches, and the dry weights (DW, 80°C). Every distinguishable axillary bud >1 mm long was considered a branch as it could give a rise of a new branch. Using a binocular loupe, the length of the largest trap (to the nearest ca. 0.2 mm) and the proportion of traps with caught prey (or brown precipitate containing humic acids or detritus) were estimated in 30 traps in the middle part of the shoots of 3-4 plants. As the individual plants had different numbers of branches, means of each of 14 plants were averaged. Means \pm SE intervals and ranges for individual plants are shown. The significant difference in parameters between the microsites was tested using a 1-way ANOVA with a Tukey HSD test for multiple comparisons. The inter-relationship of the apical shoot growth rate (ASGR, defined as the number of newly formed leaf nodes per day) of main shoots and branches was also estimated (see Adamec & Kučerová 2022).



Figure 6: Dense stand of *U. bremsii* immersed to ferric precipitates in the Suchdol Southern pool.

New branches are initiated on the apex of the main shoot and grow together with the main shoot but their ASGR may be different. When the number of mature leaf nodes from the apex is estimated in main shoots and long branches in *Utricularia* plants then the linear regression of these couples of data determines the ratio between the ASGRs of branches and main shoots. If the ratio is 1, the ASGR of both organs is the same but usually it is <1 indicating that the growth of branches is somewhat inhibited by the main shoot.

Results and discussion

Total alkalinity and electrical conductivity in the culture water were much higher than those at the three microsites in sand-pits where the waters were extremely soft and rather oligotrophic (Table 1). The Suchdol Northern pool with a denser aquatic vegetation (Fig. 5) was less oligotrophic than the Southern pool. Judging to pH values and zero total alkalinity at three microsites in both sand-pits, their free CO_2 concentration could be around two orders of magnitude lower than that in the culture and, thus, very suboptimal (espec. in the Northern pool). In general, all parameters of water chemistry in the waters are within the limits reported in the literature for *U. bremsii* (cf. Adamec 2020).

The mean lengths of main shoots of large *U. bremsii* plants were not significantly different at four microsites and varied between 34–43 cm (Table 2). The longest plants measured from 42 cm (Cep sand-pit) to 73 cm (Suchdol: Southern pool). However, the mean number of mature nodes of main

| Table 1. Water chemistry at microsites in investigated dense <i>Utricularia bremii</i> stands. TA, total alkalinity; EC, electrical conductivity. | | | | | | | |
|---|------|---------|-----------------|--------|---------------------------------|---------------------------------|--------------------|
| Microsite | pH | TA | CO ₂ | EC | NO ₃ ⁻ -N | NH ₄ ⁺ -N | PO ₄ -P |
| | | (meq/L) | (mM) | (mS/m) | (µg/L) | | |
| Culture | 6.11 | 0.73 | 1.32 | 16.3 | 13.5 | 29.2 | 1.2 |
| Cep sand-pit | 5.81 | 0.00 | – | 1.70 | 0.0 | 4.2 | 5.8 |
| Suchdol sand-pit: Southern | 6.49 | 0.00 | – | 1.61 | 0.0 | 7.2 | 8.8 |
| Suchdol sand-pit: Northern | 6.72 | 0.00 | – | 2.22 | 0.0 | 13.5 | 8.6 |

shoots (from 55-82) did not correlate with the shoot length as the shortest main shoots at Cep and Suchdol-Southern contained the most nodes. Over all, the number of main shoot nodes ranged from 40-96. The longest *U. bremii* plant in this study (73 cm) does not extend much the values reported in the literature (50-60 cm, see Adamec 2020). Moreover, the comparison of four micropopulations shows that the length of the main shoot may not be a good criterion of plant size. The long plants had on average 8.4-11.1 1st-order branches but no significant difference was found among the micropopulations though great differences occurred within each micropopulation. Unlike the mean number of 2nd-+3rd-order branches greatly differed among micropopulations and was the lowest at Cep and Suchdol-Northern (2.9-3.0). The mean number of all branches ranged from 11.4 (Suchdol-Northern) to 18.2 (Suchdol-Southern) but very high individual variability occurred within each micropopulation. The maximal length of traps was 1.2 mm at Cep, but 1.5 mm at the other microsites. The proportion of mature traps with caught prey (or a precipitate containing humic acids or detritus) was only up to 30% at Cep, but 40-60% at the other microsites.

Plant DW integrated properly the biomass of both the main shoots and all branches and expressed the size of plants best of all parameters. Marked and significant differences in mean plant DW were found between microsites (Table 2). The highest mean DW was in the plants at Suchdol-Southern (41.0 mg) and in the culture (29.9 mg) followed by Suchdol-Northern (18.2 mg) and Cep (8.8 mg). Similar to other morphometric parameters estimated, the plant DW was very variable within each micropopulation (by the factor of 3-7) and totally ranged from 4.2-103 mg. Although the number of internodes between two successive branches both on the main shoots and branches were extremely variable (total range of 1-39), the means were very similar on the same organ type among the micropopulations as well as between both types of organs for each micropopulation (Table 2). The means for main shoots were from 7.8-9.2. The linear regression of the number of leaf nodes of main shoots and branches confirmed a highly significant correlation ($P<0.001$ -0.000001; $n=8$ -23) within each micropopulation. The ratio of ASGRs for branches and main shoots was 0.733 for the culture, 0.947 at Cep, 0.667 at Suchdol Southern and 0.866 at Suchdol Northern. Thus, in all micropopulations, the apical growth rate of 1st-order branches was only 67-95% of that of main shoots. These values may express the strength of apical dominance of the main shoot apex as a sink for both mineral and organic nutrients from mature shoot segments. They are very similar to those found in closely related *U. minor* (0.83) and other aquatic carnivorous plant species (0.65-0.85, see Adamec & Kučerová 2022) and suggest that this relationship between the ASGRs can be generalized for this plant group. However, the significant

Table 2. Morphometric characteristics of robust *Utricularia bremii* plants in culture in the Institute of Botany at Třeboň and in three shallow oligotrophic pools in two sand-pits in S Bohemia, Czech Republic. Numbers of internodes between two branches on the main shoot and branches are shown. DW, dry weight. Means \pm SE intervals (*italics*) based on averages for individual plants are shown, $n=14$. Range of values shown for individual plants. Different letters within the columns for variants denote statistically significant difference at $P<0.05$ (1-way ANOVA).

| Microsite | Main shoot length (cm) | Main shoot nodes | Plant DW (mg) | Number of branches per plant | | | Internodes between two branches | |
|----------------------------|------------------------|-------------------|--------------------|------------------------------|--|--------------------|---------------------------------|------------------|
| | | | | 1 st -order | 2 nd -+3 rd -order | All | Main shoots | Branches |
| Culture | 38.3 ^a | 55.1 ^a | 29.9 ^{ac} | 9.1 ^a | 6.2 ^{ab} | 15.3 ^{ab} | 7.8 ^a | 8.3 ^a |
| | ± 2.8 | ± 2.9 | ± 3.1 | ± 0.8 | ± 0.9 | ± 1.6 | ± 0.5 | ± 0.3 |
| | 23.2–64.5 | 40–75 | 11.4–51.3 | 6–15 | 2–15 | 8–25 | 1–17 | 3–17 |
| Cep sand-pit | 34.1 ^a | 81.7 ^b | 8.8 ^b | 11.1 ^a | 2.9 ^a | 14.0 ^{ab} | 7.8 ^a | 8.5 ^a |
| | ± 1.2 | ± 3.0 | ± 0.8 | ± 1.2 | ± 0.8 | ± 1.6 | ± 1.0 | ± 1.1 |
| | 25.2–41.5 | 52–96 | 4.2–13.6 | 3–19 | 0–10 | 3–25 | 1–39 | 1–27 |
| Suchdol sand-pit: Southern | 42.8 ^a | 59.4 ^a | 41.0 ^a | 9.6 ^a | 8.6 ^b | 18.2 ^a | 8.1 ^a | 7.8 ^a |
| | ± 2.9 | ± 2.7 | ± 6.8 | ± 0.8 | ± 1.6 | ± 2.1 | ± 0.5 | ± 0.3 |
| | 34.1–73.0 | 45–82 | 15.6–103 | 6–16 | 1–20 | 7–32 | 2–25 | 3–16 |
| Suchdol sand-pit: Northern | 37.5 ^a | 64.4 ^a | 18.2 ^{bc} | 8.4 ^a | 3.0 ^a | 11.4 ^b | 9.2 ^a | 7.7 ^a |
| | ± 2.3 | ± 3.0 | ± 1.9 | ± 0.6 | ± 0.6 | ± 1.1 | ± 0.3 | ± 0.5 |
| | 28.7–62.0 | 53–94 | 9.0–31.8 | 4–12 | 0–7 | 6–18 | 3–16 | 2–16 |

differences between four *U. bremii* micropopulations indicate that physiological relationships between main shoots and branches are modulated by environmental conditions such as CO₂ or prey availability.

The most of the selected *U. bremii* plants in this study bore senescent shortened turion leaves at their shoot bases at all microsites. This means that these plants started their seasonal, spring growth from turions, but not from separated branches later in the season. The comparison of morphometric data on robust *U. bremii* (Table 2) and *U. minor* plants (Adamec & Kučerová 2022) confirms that on the level of length and number of nodes of the main shoot, number of 1st-order branches and plant DW, both species are very similar to each other as the mean as well as individual values greatly overlap though *U. bremii* in this study was somewhat more branched. However, an evident difference between both closely related species was found in the branching rate of main shoots and branches: in *U. minor*, the mean values were 12.2 and 16.8 internodes, respectively (Adamec & Kučerová 2022, cf. Table 2). The lower branching rate in *U. minor* could be due to frequent flowering and seed set since in an ecologically similar *Aldrovanda vesiculosa*, developing flowers competed with shoot apices and reduced markedly the branching rate (Cross *et al.* 2016). Moreover, it is well known in several *Utricularia* species and *Aldrovanda* that branching rate depends strongly on CO₂ or prey availability (Adamec 2018). Thus, put together, these plants can regulate not only the number of formed branches, but also their growth rate. At four *U. bremii* microsites, a new branch

was initiated on average after each 7.8-9.2 internodes on the main shoots (Table 2). Considering an ASGR of 2.4 internodes/day in *U. breinii* (Adamec 2011), a new branch is theoretically initiated as early as every ca. 3.3-3.8 days, while it can be every ca. 5.1 days in *U. minor* (Adamec & Kučerová 2022). Thus, *U. breinii* could propagate faster.

Plant DW could be considered the best criterion of size and fitness of *U. breinii*. Out of four micropopulations, the smallest and the most slender shoots were clearly at the Cep sand-pit, which was evidently the most oligotrophic of all microsites (Table 1) and where the plants also caught the minimum of prey. This result may be confirmed by a greenhouse-growth experiment (Adamec 2011) that optimal growth conditions for this species include mainly relatively high CO₂ concentration and prey availability but low cover of aquatic plants, while water hardness is not important. As concluded also in this study, optimal ecological factors for *U. breinii* can be met in shallow (10-25 cm), well-lit pools in oligo-mesotrophic sand-pits which represent one out of optimal habitats for this species (Adamec 2020). Moreover, eutrophic waters are excluded for this species. It should be added that no *U. breinii* plants flowered at the four microsites at the sampling time due to water level fluctuations before. It has been observed in shallow Czech sand-pits repeatedly (Adamec 2020) that *U. breinii* flowers prolifically only in very shallow pools (1-5 cm), while no flowering usually occurs in deeper waters (>12-15 cm).

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