

# Peculiarities of growth and nutrition of aquatic carnivorous plants

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## AIMS OF THE LECTURE:

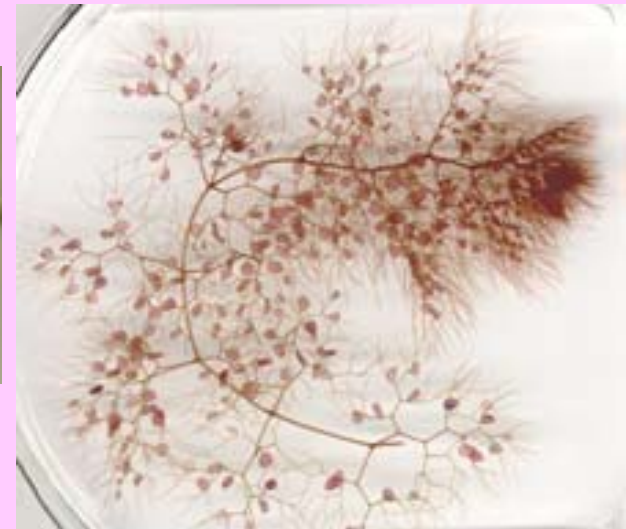
to summarize recent items of ecophysiological knowledge of aquatic carnivorous plants (**ACPs**) relating to their growth, photosynthesis, and mineral nutrition.

**Aquatic carnivorous plants:** about 50 species of 2 genera:

- *Aldrovanda vesiculosa* (Droseraceae): snapping trap



- *Utricularia* (Lentibulariaceae): suction trap



- 8 species of ACPs in the Czech flora (6 critically endangered !)

# 1) Characterization of habitats of ACPs

1. shallow standing dystrophic waters (+ humic acid + tannins);
2. usually low concentration of mineral N, P, and K;
3. high  $[\text{NH}_4^+]$  :  $[\text{NO}_3^-]$  ratio in the waters;
4. usually high  $[\text{CO}_2]$  in the waters.

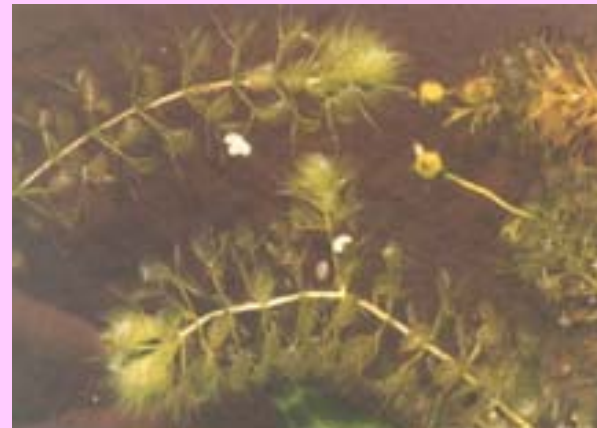


## 2) Linear shoot structure and growth characteristics

- all ACP species are rootless: either free floating below the water surface or loosely attached to the sediment; many species are amphibious;
- mostly linear shoots with modular structure: shoots either **monomorphic** (homogenous, non-differentiated) with traps or **dimorphic** (heterogenous, differentiated into **photosynthetic** and **carnivorous**);



- “conveyer belt” shoot growth system: permanent, very rapid apical growth (new 1-3 leaf whorls.d<sup>-1</sup>), permanent basal shoot ageing and decay => ~constant shoot length;
- allocation of a new plant biomass to branching or flowering;
- branching is rather regular under optimum conditions => branching rate (leaf whorls.branch<sup>-1</sup>) and frequency (days.branch<sup>-1</sup>): branching frequency as a criterion of growth rate;
- RGR of ACPs is very high:  $T_2$  (doubling time of biomass or shoot apices) of 2 ACP species: 8-20 d in summer (in contrast, RGR of terrestrial carnivorous plants /3 *Drosera* spp./ is low:  $T_2$  ~40-50 d).



Very rapid apical growth of rootless ACPs requires:

- high photosynthetic rate or efficient re-utilization of carbohydrates from senescent shoots;
- efficient re-utilization of mineral nutrients from senescent shoots;
- catching of prey.

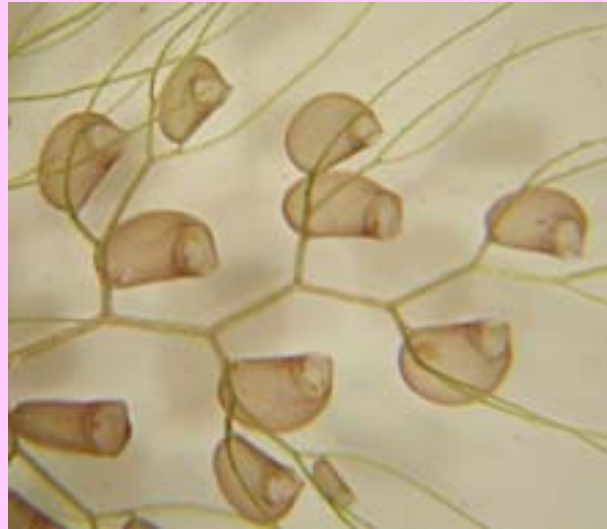
Growth characteristics of ACPs reflect very steep physiological polarity along shoots of ACPs. The polarity includes:

- tissue mineral nutrient content;
- carbohydrate content;
- metabolic activity (photosynthesis);
- presumably also phytohormone content.



### 3) Photosynthetic characteristics

- C<sub>3</sub> species, strict CO<sub>2</sub> users: CO<sub>2</sub> compensation points: *Aldrovanda*: 5-11 μM; *Utricularia* spp.: 2-13 μM;
- very high PN of shoots (upper range within submerged plants: 30-110 mmol.kg<sup>-1</sup><sub>FW</sub>.h<sup>-1</sup>);
- low PN but high RD of traps (high metabolic costs of carnivory): total trap RD in 3 *Utricularia* species: ~60-68 % of total plant RD.



**PN** and **RD** ( $\text{mmol.kg}^{-1}_{\text{FW.h}^{-1}}$ ) of trapless leaves/shoots and traps of photosynthetic shoots of ACPs under optimum conditions ( $20\text{ }^{\circ}\text{C}$ ,  $300\text{-}400\ \mu\text{mol.m}^{-2}.\text{s}^{-1}$  PAR,  $0.2\ \text{mM CO}_2$ ).

Species	<b>PN</b>		<b>RD</b>	
	Leaves	Traps	Leaves	Traps
<i>Aldrovanda</i>	70-90	54	10	--
<i>Utricularia</i> spp.	40-120	5-15	3-5	7-8.5





#### 4) Mineral nutrition of ACPs

1. ACPs are adapted to preferential uptake of  $\text{NH}_4^+$  over  $\text{NO}_3^-$  from equimolar solutions;
2. high efficiency of N uptake from prey: >83 % in *U. vulgaris* from mosquito larvae;
3. efficient N and P re-utilization from senescent ACP shoots but loss of K, Ca, and Mg:

#### Re-utilization of mineral nutrients from senescent shoots in 2 species of ACPs (related to apices). Mean tissue nutrient content shown in % DW.

Shoot segments	<i>Aldrovanda</i> (culture)					<i>U. australis</i> (30 field sites)				
	N	P	K	Ca	Mg	N	P	K	Ca	Mg
apex	1.31	0.48	1.86	0.17	0.16	3.29	0.53	3.14	0.12	0.27
1-6 whorls	0.98	0.30	2.11	0.32	0.21	2.68	0.35	4.16	0.19	0.33
old whorls	0.10	0.10	2.30	0.75	0.16	1.40	0.10	4.61	0.81	0.37
<b>Re-util. %</b>	<b>92</b>	<b>79</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>57</b>	<b>81</b>	<b>0</b>	<b>0</b>	<b>0</b>

- 1) efficient N and P re-utilization from summer shoots to turions (>90 % in *Aldrovanda*).

## 5) Importance of carnivory for ACP growth

Effect of addition of zooplankton, *Carex* rhizomes, or a combination of the two on *Aldrovanda* growth in a greenhouse (diluted mineral nutrient solution, 27 d). Data shown in % of the controls.

Treatment	Plant length	DW
<b>Controls</b>	<b>100</b>	<b>100</b>
+Zooplankton	184	269
+ <i>Carex</i>	195	250
+Zooplankton + <i>Carex</i>	256	334

Effect of feeding on zooplankton on *Aldrovanda* and *U. australis* growth (15-17 d) from two different outdoor experiments. AGR, apical growth rate. Tissue nutrient content shown in 1<sup>st</sup>-6<sup>th</sup> (*AL*) or 7<sup>th</sup> leaf whorls (*UA*).

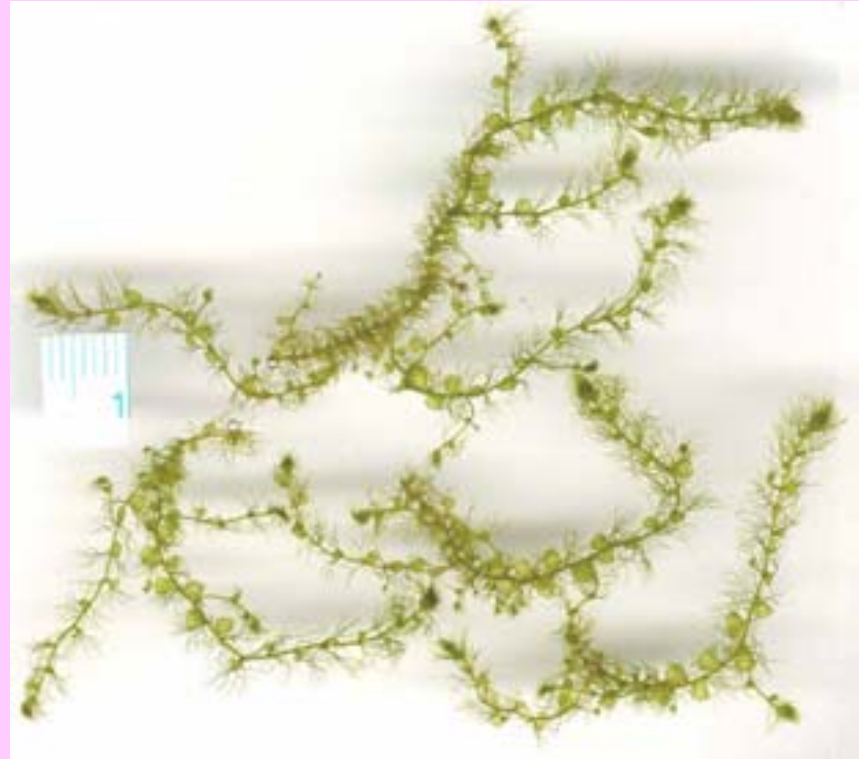
Treatment	DW (mg)	Length (cm)	T <sub>2</sub> (d)	AGR (wh.d <sup>-1</sup> )	Branch. .plant <sup>-1</sup>	N	P	K	Ca
						(% DW)			
<b><i>Aldrovanda</i></b>									
Unfed	8.2	5.4	44.5	0.60	0.00 !	0.85	0.25	2.84	0.81
Fed	15.7	8.7	12.8	0.98	0.69	0.79	0.20	2.93	0.67
<b><i>U. australis</i></b>									
Unfed	--	28.0	--	0.87	0.50	1.50	0.17	--	--
Fed	--	38.9	--	1.16	0.64	0.81	0.13	--	--



- => catch of prey is crucial for the growth rate of ACPs (branching);
- the effect of catching of prey on photosynthesis of ACPs is unclear;
- catching of prey decreased chlorophyll content in leaves of ACPs;
- *U. macrorhiza* (WI, USA) took up up to 75 % of N gain from prey, *U. foliosa* (a barren site, FL, USA) only 0.9 % N and 3.5 % P;
- model case of catching one prey.d<sup>-1</sup> (DW ~25 µg, 10 % N, 1 % P) by:  
*Aldrovanda* (DW 30 mg, T<sub>2</sub> 15 d): 15 % N and 4 % P of daily gain, but at zero RGR: 100 % N and 16 % P;
- *U. australis* (DW 170 mg, T<sub>2</sub> 15 d): 0.62 % N and 0.56 % P of daily gain, but at zero RGR: 1.8 % N and 2.6 % P.

## 6) Regulation of the proportion of trap biomass to the total one (i.e., investment in carnivory)

- traps of ACPs include structural, mineral, and metabolic costs: trap proportion: ~10-62 % of total DW (usually 25-50 %);
- => need to regulate the trap proportion flexibly according to ambient ecological conditions;



## Ecological factors changing the investment in carnivory (IIC) in ACPs.

Species	Ecological factor	Change in IIC	Remark
<i>U. foliosa</i>	total ion concent.	-	streaming water
-""-	[NO <sub>3</sub> <sup>-</sup> ]	--	-""-
-""-	catching of prey	++	-""-
-""-	prey availability	-	-""-
<i>U. macrorhiza</i>	total ion concent.	++	number of traps
-""-	catching of prey	-	-""-
<i>U. vulgaris</i>	[PO <sub>4</sub> ]	-	laboratory: 12 °C
-""-	[PO <sub>4</sub> ]	-	field data: Poland
<i>U. vulgaris</i>	irradiance	-	field exp., no prey
-""-	catching of prey	-	field experiment
<i>U. australis</i>	[CO <sub>2</sub> ]	++	field data: Třeboň
-""-	catching of prey	--	-""-

1. => inverse proportional relationship between mineral nutrient availability and trap proportion;
2. **negative feedback** of the regulation of trap proportion found in field-grown *U. australis*: **tissue N content in young shoots** acts as the key regulatory factor: all nutritional influences decreasing shoot N content increase trap proportion and *vice versa*.
3. in *U. vulgaris*: probably shoot P content.

## 7) Conclusions

- The main benefit of carnivory is the gain of N and P from prey.
- As carnivory increases neither PN per unit DW nor leaf nutrient content, the physiological response to carnivory neither takes place in adult leaves/shoots nor stimulates PN per unit DW (as suggested by Givnish et al. 1984).
- Instead, it is possible to hypothesize that the response to carnivory, leading to growth stimulation, takes place in young, developing cells and tissues in shoot apices. Due to increased N and P availability in apical meristems, growth processes like cell division, DNA replication, transcription, proteosynthesis, etc., might be stimulated.

## 8) Inspiration for further research on ACPs.....



- does carnivory in ACPs lead to a stimulation of mineral nutrient uptake by shoots from ambient water (analogy with terrestrial CPs)?
- what is the efficiency of absorption of mineral (organic) nutrients from prey?
- what is the role of organic substances (incl. humic acids, tannins) for the growth and development of ACPs?
- where are phytohormones produced in rootless ACPs and how do they function?

