Peculiarities of growth and nutrition of aquatic carnivorous plants

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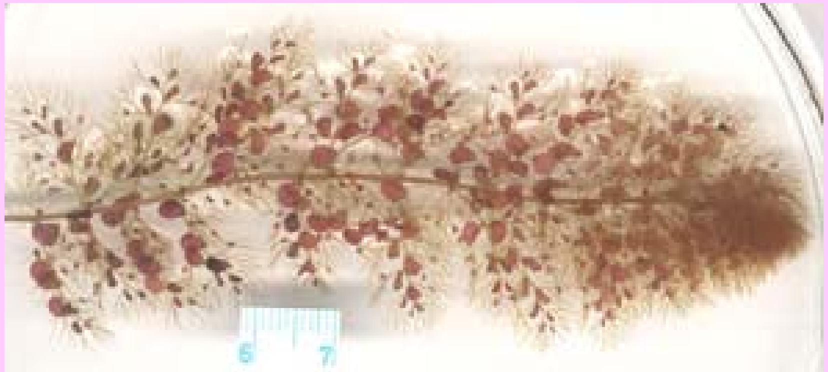
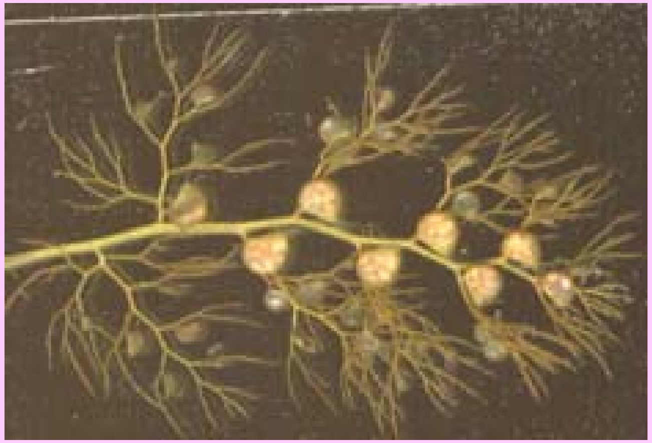




AIMS OF THE LECTURE:

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

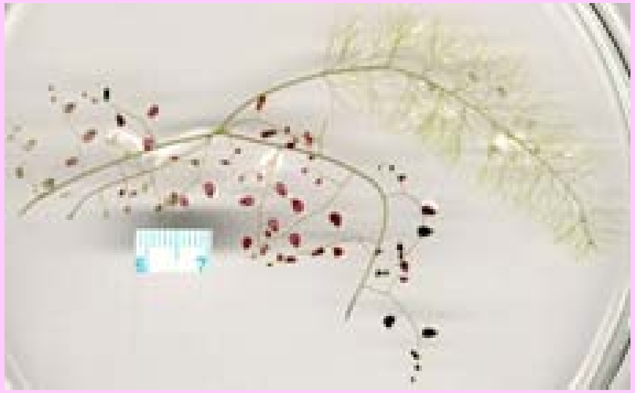
1. shallow standing dystrophic waters (+ humic acid + tannins);
2. usually low concentration of mineral N, P, and K;
3. high $[NH_4^+] : [NO_3^-]$ ratio in the waters;
4. usually high $[CO_2]$ in the waters.





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^{-1}), 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.$branch^{-1}$) and frequency (days.$branch^{-1}$): 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:

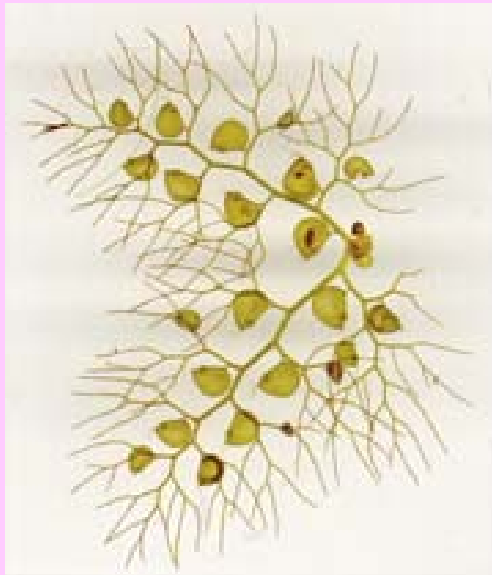
- tissue mineral nutrient content;
- carbohydrate content;
- metabolic activity (photosynthesis);
- presumably also phytohormone content.

3) Photosynthetic characteristics

• C_3 species, strict CO_2 users: CO_2 compensation points: *Aldrovanda*: 5-11 µM; *Utricularia* spp.: 2-13 µM;

• very high PN of shoots (upper range within submerged plants: 30-110 $mmol.kg^{-1}_{FW}.h^{-1}$);

• 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 (mmol.kg^{-1}_{FW}.h^{-1}) of trapless leaves/shoots and traps of photosynthetic shoots of ACPs under optimum conditions (20 ^{o}C, 300-400 μmol.m^{-2}.s^{-1} PAR, 0.2 mM CO_2).

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

4) Mineral nutrition of ACPs

1. ACPs are adapted to preferential uptake of NH_4^+ over 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	*Aldrovanda* (culture)					*U. australis* (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
Re-util. %	**92**	**79**	**0**	**0**	**0**	**57**	**81**	**0**	**0**	**0**

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
Controls	100	100
+Zooplankton	184	269
+*Carex*	195	250
+Zooplankton +*Carex*	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^{st}-6^{th} (*AL*) or 7^{th} leaf whorls (*UA*).

Treatment	DW (mg)	Length (cm)	T_2 (d)	AGR ($wh.d^{-1}$)	Branch. $.plant^{-1}$	N	P	K	Ca
						(% DW)			
Aldrovanda									
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
U. australis									
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^{-1} (DW ~25 µg, 10 % N, 1 % P) by:

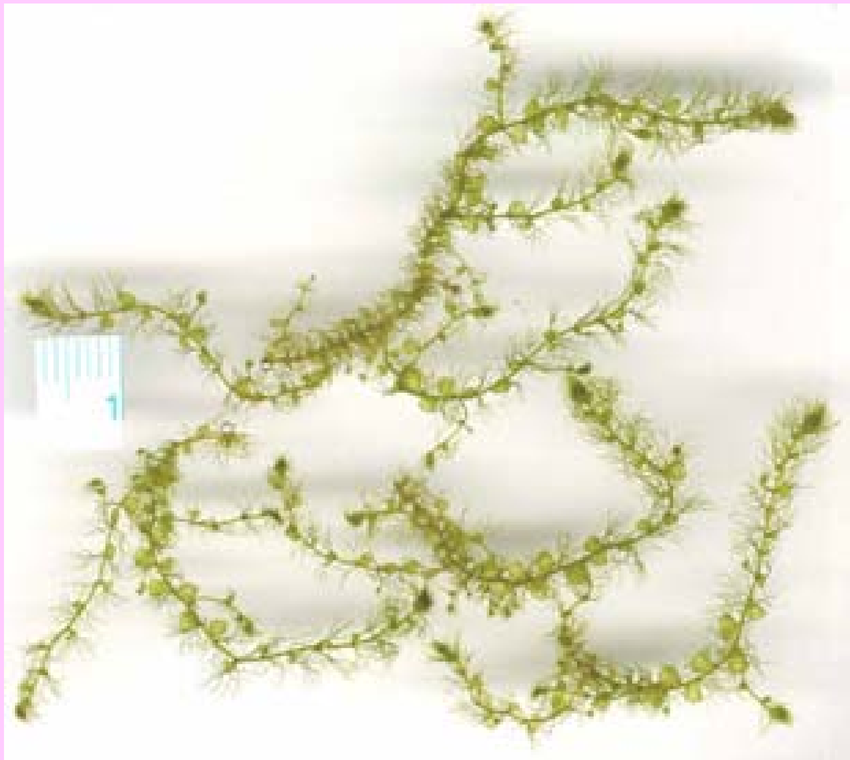
Aldrovanda (DW 30 mg, T_2 15 d): 15 % N and 4 % P of daily gain, but at zero RGR: 100 % N and 16 % P;

U. australis (DW 170 mg, T_2 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
U. foliosa	total ion concent.	**-**	streaming water
-""-	[NO_3^-]	**- -**	-""-
-""-	catching of prey	++	-""-
-""-	prey availability	**-**	-""-
U. macrorhiza	total ion concent.	**++**	number of traps
-""-	catching of prey	**-**	-""-
U. vulgaris	[PO_4]	**-**	laboratory: 12 ^{o}C
-""-	[PO_4]	**-**	field data: Poland
U. vulgaris	irradiance	**-**	field exp., no prey
-""-	catching of prey	-	field experiment
U. australis	[CO_2]	**++**	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?