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Mineral cost of carnivory in aquatic carnivorous plants

Lubomír Adamec*

Institute of Botany of the Academy of Sciences of the Czech Republic, Section of Plant Ecology, Dukelská 135, CZ-379 82 Třeboň, Czech Republic

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ABSTRACT

Tissue N, P, K, Ca, and Mg content was estimated in traps and photosynthetic and carnivorous shoots in five aquatic carnivorous plant species from an outdoor culture: *Aldrovanda vesiculosa*, *Utricularia vulgaris*, *U. reflexa*, *U. intermedia*, and *U. stygia*, for the determination of the mineral cost of carnivory. In three species with monomorphic shoots (*A. vesiculosa*, *U. vulgaris*, *U. reflexa*), tissue P and K content in traps was significantly higher than that in their photosynthetic shoots, whereas N content was about the same. In *U. stygia* and *U. intermedia* with dimorphic shoots, tissue N and P content was markedly the highest in photosynthetic shoots followed by traps, while it was lowest in carnivorous shoots. In all five species, trap K content was significantly (2–4 times) higher than that in photosynthetic and carnivorous shoots. In all species, the values of the mineral cost of carnivory – the proportion of mineral nutrient amount contained in traps or carnivorous shoots to that in the total plant biomass – were within 19–61% for N, 33–76% P, 51–78% K, 26–70% Ca, and 34% for Mg. A new concept of the ecological cost-benefit relationships of plant carnivory, based on the mineral benefit of prey capture and mineral costs associated with trap production, is introduced for aquatic carnivorous plants. The evolution of this plant group is considered to show the optimization of these mineral cost-benefit relationships.

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Introduction

Aquatic carnivorous plants comprise the species *Aldrovanda vesiculosa* L. (Droseraceae) and about 50 species of the genus *Utricularia* L. (Lentibulariaceae; Juniper et al., 1989; Taylor, 1989). Rootless aquatic carnivorous plants usually grow in shallow standing dystrophic waters, which are predominantly nutrient poor in N and P, also usually in K (Adamec, 1997a, 2008a; Guisande et al., 2007). They take up all necessary nutrients either directly from water or from prey. Their principal adaptations include carnivory, efficient nutrient re-utilization from senescent shoots, and, probably, a very high nutrient uptake affinity from water (Adamec, 2000, 2008a; Englund and Harms, 2003; Kosiba, 1992a,b).

In aquatic *Utricularia* species, the proportion of the total shoot biomass invested in traps (i.e., structural investment in carnivory) is considerable and can range from 10% to 62% in various species (Adamec, 2008a; Friday, 1992; Knight, 1992; Porembski et al., 2006). However, the plants are able to change the proportion of shoot biomass invested in traps according to habitat factors: particularly water chemistry, prey availability, and level of irradiance (Adamec, 2007, 2008a; Bern, 1997; Englund and Harms, 2003; Guisande et al., 2000, 2004; Knight and Frost, 1991; Knight, 1992; Manjarrés-Hernández et al., 2006; Richards, 2001). An inverse

proportional relationship between shoot N and P content and investment in carnivory was found in *U. foliosa* (Bern, 1997) and has recently been confirmed for tissue N content in young shoot segments of *U. australis* (Adamec, 2008a). In the latter study, all nutritional influences which could increase shoot N content, decreased the investment in carnivory, and *vice versa*. Thus, shoot N content in this species acts as a key endogenous factor regulating structural investment in trap biomass through a negative feedback mechanism. However, shoot P rather than N content has been found to regulate the investment in carnivory in *U. vulgaris* (Kibriya and Jones, 2007).

Utricularia traps are physiologically very active organs and their respiration rate per unit biomass exceeds that of leaves 1.7–3.0 times (Adamec, 2006). In *U. australis*, the total trap respiration amounted to 67% of the plant's total respiration as the energetic cost. However, traps of aquatic *Utricularia* species represent not only considerable structural and energetic (metabolic) costs, but also a mineral cost. As recently found by Adamec (2008a) in field-grown *U. australis*, tissue P and K in traps was markedly greater than that in leaves in adult shoot segments, while the relations were opposite for N, Ca, and Mg content. Thus, in this species, mineral investment in carnivory was 30% of plant's total N, but 54% of its P and 51% of K.

The aim of this study was to estimate tissue N, P, K, Ca, and Mg content of traps and photosynthetic and carnivorous shoots in five aquatic carnivorous plant species: *Aldrovanda vesiculosa* (non-differentiated, homogeneous shoots, snapping traps), *Utricu-*

* Tel.: +420 384 721156; fax: +420 384 721136.
E-mail address: adamec@butbn.cas.cz.

Utricularia vulgaris L., *U. reflexa* Oliver (non-differentiated shoots, suction traps), *U. intermedia* Hayne, and *U. stygia* Thor (syn. *U. ochroleuca* Hartm. s. l.; dimorphic, heterogeneous shoots) and, on the basis of trap proportion in plant biomass, to evaluate the mineral cost of carnivory.

Materials and methods

Experimental plants

All plants used were grown in outdoor cultures and were used for nutrient analyses at the peak of the growing season on 15–16 August 2007. *A. vesiculosa* (collected originally from E Poland), *U. vulgaris* (collected originally from S Moravia, Czech Rep.), and *U. stygia* (collected originally from Třeboň region, Czech Rep.) were grown in the same 2.5 m² plastic container in 25–30 cm deep water (see Adamec, 1997b). *U. intermedia* (collected originally from Třeboň region) was grown similarly in a 0.8 m² plastic container in 25 cm deep water, while *U. reflexa* (collected originally from Zambia) was grown in a 3-l aquarium bathed in a 2 m² plastic container for cooling. All plants of a certain species represent pseudoreplicates. *Carex* litter as substrate covered the bottom of the containers and the aquarium in about 2–3 cm layer. All cultures were partly shaded and the PAR irradiance on the plant level was about 40–50% of that in the open. Fine zooplankton were added repeatedly (1–2 times weekly, mainly *Cyclops*, *Eydiaptomus*, ostracods) to all cultures to gently feed the plants. The containers mimicked a shallow dystrophic pool in which all species occur naturally. According to water chemistry, water in all cultures can be considered oligomesotrophic and dystrophic (see Adamec, 1997b, 2000, 2008a). Shortly, the pH of the cultivation media ranged from 6.8 to 7.3, total alkalinity from 0.8 to 1.1 mequiv. l⁻¹, free CO₂ concentration from 0.1 to 0.2 mM, NO₃⁻-N from 5 to 30 µg l⁻¹, NH₄⁺-N from 10 to 30 µg l⁻¹, and PO₄-P from 10 to 17 µg l⁻¹.

At the time of sampling, all five plant species were adult and their younger shoot segments were free of periphytic algae. The dominant part (>90%) of mature traps in all species used was without macroscopic prey. Young shoot segments with traps from 4th to 5th mature leaf whorls were excised in *A. vesiculosa* (trap size 3.5–5 mm), leaves from 10th to 12th mature shoot nodes in *U. vulgaris* (trap size 1.5–4 mm), shoot segments from 4th to 10th mature shoot nodes in *U. reflexa* (trap size 3–7 mm), and photosynthetic shoot segments 5–6 cm long between cm 2 and 8 from the apex and apical carnivorous shoot segments 4–6 cm long were excised in *U. stygia* and *U. intermedia* (trap size 2–4 mm). In each plant species, all traps were separated from shoots or leaves using fine scissors. Excised traps without prey and the shoot segments or leaves without traps were rinsed shortly with distilled water, blotted dry (the fluid was thoroughly pressed out from traps), and dried at 80 °C in pooled samples (ca. 4–5 mg dry weight, DW, 50–80 traps) from 1 to 4 plants. Five parallel samples were obtained for each species and organ type. In *A. vesiculosa* and *U. reflexa*, the proportion of the shoot segment DW invested in trap DW was estimated in a parallel pooled sample, while the data for the other species were taken from the literature (Friday, 1992; Adamec, 2007, 2008a).

Tissue nutrient content and statistical treatment

Dry plant material was mineralised using concentrated acids, diluted and analysed for N, P, K, Ca, and Mg content (for all analytical details see Adamec, 2002). For N analyses, 0.7–0.9 mg of DW of traps or shoots was mineralised with H₂SO₄, 1.0–1.5 mg DW with HClO₄ for P, and 2.0–3.0 mg with HNO₃ for metallic cation analyses. N and P were determined colorimetrically by an automatic FIAstar 5010 Analyzer (Tecator, Sweden), while metallic cation concen-

trations were estimated by atomic absorption flame spectrometry using an analyzer SpectrAA 640 (Varian Techtron, Australia). Five replications were used for each variant. Throughout the paper, the mean with standard error is provided wherever possible. Significant differences between different organs within single species were evaluated by a one-way ANOVA (Tukey HSD test). Significant differences between all five species (regardless of the genus) and photosynthetic shoots and traps (represented in all species) were evaluated by a factorial two-way ANOVA (species and organ type as fixed effects). For *U. stygia* and *U. intermedia* with three organ types, a two-way ANOVA was used to compare the differences in tissue chemistry between the certain organ type and the species. The values of mineral cost of carnivory, defined as the proportion of the amount of a given nutrient in traps or carnivorous shoots bearing traps to the total amount of that nutrient in the plant, were calculated from the measured values of tissue chemistry and from the values of structural investment in carnivory, either measured directly or taken from the literature (see above).

Results

In three species with monomorphic shoots (*A. vesiculosa*, *U. vulgaris*, *U. reflexa*), tissue P and K content in their traps was statistically significantly higher than that in their photosynthetic shoots (leaves), whereas tissue N content was about the same (Table 1). Unlike *A. vesiculosa*, in both *Utricularia* species, tissue Ca and Mg content was markedly and significantly lower in traps as compared to photosynthetic shoots. In *U. stygia* and *U. intermedia* with dimorphic shoots, tissue N and P content was markedly the highest in their photosynthetic shoots followed by traps, while it was the lowest in carnivorous shoots. However, the content of metallic cations in both species was quite different. Tissue K content in traps was significantly (ca. 2.4–4 times) higher than that in photosynthetic and carnivorous shoots, while the distribution of both Ca and Mg was quite opposite: the highest contents were in carnivorous or photosynthetic shoots but significantly lower in traps. In all five species, the N:P stoichiometry (based on weight ratios) was always the greatest in photosynthetic shoots (5.5–16.0) and the lowest in traps (4.1–8.2), while the K:Ca stoichiometry was quite opposite: the greatest in traps and the lowest in photosynthetic and carnivorous shoots (Table 1). As revealed by two-way ANOVA for photosynthetic shoots and traps within all five species, a highly significant difference in all parameters of tissue chemistry or nutrient stoichiometry was found between species and the same (except for a non-significant difference for P content) was the case also for the differences between both organs (Table 1). Except for a non-significant difference for N:P stoichiometry, the interaction between species and organ type was also highly significant for all parameters estimated. In *U. stygia* and *U. intermedia* with dimorphic shoots, the differences in all estimated parameters were found to be significant (two-way ANOVA, $p < 0.05$) both between the two species (only except for tissue Mg content and K:Ca stoichiometry) and the organ type. Also the species × organ type interaction was significant for all parameters (data not shown). Overall, the values of the tissue nutrient content in aquatic carnivorous plants show great differences between different organ types. On average, the greatest differences exist for N, K, and Ca content and N:P and K:Ca stoichiometry, while the smallest for P and Mg content (Table 1).

The mean values of structural investment in carnivory (only traps in species with monomorphic shoots or also carnivorous shoots with traps in species with dimorphic shoots), used for calculation of mineral cost of carnivory, ranged from 38–63% of total shoot biomass for six aquatic species (Table 2). The values of mineral cost of carnivory amounted to 19–61% for N, 33–76% P, 51–78%

Table 1
Comparison of tissue nutrient content in photosynthetic shoots or leaves (PS) without traps, in carnivorous shoots without traps (CA), and in traps without prey (TR) from young, adult shoots of aquatic carnivorous plants.

Species	Organ	Tissue nutrient content (% DW)						
		N	P	K	Ca	Mg	N:P	K:Ca
<i>A. vesiculosa</i>	PS	1.03 ± 0.28	0.063 ± 0.001 ^a	1.12 ± 0.11 ^a	0.33 ± 0.03 ^a	0.062 ± 0.004 ^a	16.0 ± 4.1	3.37 ± 0.08 ^a
	TR	0.94 ± 0.15	0.11 ± 0.001 ^b	2.31 ± 0.04 ^b	0.46 ± 0.02 ^b	0.13 ± 0.004 ^b	8.24 ± 1.42	5.08 ± 0.15 ^b
<i>U. vulgaris</i>	PS	1.15 ± 0.14	0.12 ± 0.003 ^a	2.57 ± 0.10 ^a	0.88 ± 0.02 ^a	1.00 ± 0.03 ^a	9.80 ± 0.94	2.95 ± 0.15 ^a
	TR	1.02 ± 0.12	0.13 ± 0.002 ^b	5.65 ± 0.24 ^b	0.50 ± 0.02 ^b	0.69 ± 0.03 ^b	7.61 ± 0.92	11.4 ± 0.33 ^b
<i>U. reflexa</i>	PS	0.74 ± 0.02	0.094 ± 0.005 ^a	1.66 ± 0.16 ^a	1.88 ± 0.05 ^a	0.38 ± 0.008 ^a	7.91 ± 0.36 ^a	0.89 ± 0.09 ^a
	TR	0.73 ± 0.07	0.16 ± 0.005 ^b	3.74 ± 0.11 ^b	0.90 ± 0.02 ^b	0.26 ± 0.005 ^b	4.62 ± 0.40 ^b	4.18 ± 0.08 ^b
<i>U. stygia</i>	PS	2.66 ± 0.14 ^a	0.31 ± 0.01 ^a	2.05 ± 0.15 ^a	0.86 ± 0.02 ^a	0.30 ± 0.01 ^a	8.80 ± 0.70 ^a	2.40 ± 0.21 ^a
	CA	0.58 ± 0.06 ^b	0.14 ± 0.02 ^b	1.98 ± 0.14 ^a	1.21 ± 0.03 ^b	0.31 ± 0.005 ^a	4.54 ± 0.86 ^b	1.65 ± 0.15 ^a
	TR	0.86 ± 0.04 ^b	0.21 ± 0.004 ^c	4.82 ± 0.19 ^b	0.55 ± 0.01 ^c	0.17 ± 0.004 ^b	4.12 ± 0.21 ^b	8.77 ± 0.35 ^b
<i>U. intermedia</i>	PS	1.16 ± 0.07 ^a	0.21 ± 0.07 ^a	1.81 ± 0.05 ^a	1.11 ± 0.07 ^a	0.29 ± 0.01 ^a	5.54 ± 0.39 ^a	1.66 ± 0.13 ^a
	CA	0.43 ± 0.01 ^b	0.085 ± 0.007 ^b	1.22 ± 0.14 ^b	1.19 ± 0.02 ^a	0.27 ± 0.01 ^a	5.20 ± 0.40 ^{ab}	1.03 ± 0.12 ^a
	TR	0.67 ± 0.02 ^c	0.17 ± 0.006 ^c	4.87 ± 0.17 ^c	0.45 ± 0.02 ^b	0.23 ± 0.006 ^b	3.86 ± 0.14 ^b	11.0 ± 0.61 ^b
Mean ± SE	PS	1.36 ± 0.15	0.16 ± 0.02	1.84 ± 0.11	1.01 ± 0.10	0.41 ± 0.06	9.36 ± 0.95	2.25 ± 0.19
	Ca	0.51 ± 0.04	0.11 ± 0.01	1.60 ± 0.16	1.20 ± 0.02	0.29 ± 0.01	4.87 ± 0.05	1.34 ± 0.14
	TR	0.85 ± 0.05	0.16 ± 0.01	4.28 ± 0.25	0.57 ± 0.03	0.29 ± 0.04	5.84 ± 0.53	–
Species	–	**	**	**	**	**	*	**
Organ	–	**	ns	**	**	**	*	**
Species × organ	–	**	**	**	**	**	ns	**

Means ± SE are shown; $n = 5$. On the bottom, means ± SE for different organ types pooled for all plant species are shown. Different letters denote statistically significant difference (one-way ANOVA, HSD-Tukey test) between different organs within each species at $p < 0.05$; unlabelled cases are non-significant. Significance (between all species, organ/only PS and TR/, and species × organ interaction; two-way ANOVA) is shown in the bottom of the table.

^{ns} $p > 0.05$.

* $p < 0.0001$.

** $p < 0.00001$.

Table 2
The comparison of mineral cost of carnivory, as proportion of the amount of a given nutrient in traps (TR) or carnivorous shoots bearing traps (CA) to the total plant amount, in aquatic carnivorous species on the basis of data from Table 1.

Species	Organ	IIC (%)	N					P					K					Ca					Mg				
			(% of total plant content)																								
<i>A. vesiculosa</i>	TR	62.9	60.6	75.5	77.8	70.1	78.1																				
<i>U. vulgaris</i>	TR	50.0	47.0	53.6	68.7	36.2	40.9																				
<i>U. reflexa</i>	TR	47.5	47.4	62.8	67.1	30.1	38.3																				
<i>U. australis</i> ^a	TR	38.4	30.2	53.7	51.0	26.3	34.0																				
<i>U. stygia</i>	TR	23.8	11.5	20.3	42.6	15.2	14.9																				
	CA	45.7	18.7	32.7	58.7	45.9	40.4																				
<i>U. intermedia</i>	TR	27.5	21.5	28.1	53.2	13.0	23.0																				
	CA	50.6	33.3	39.6	64.5	42.1	45.9																				

^a Literature data on tissue nutrient content (Adamec, 2008a) were used. IIC, structural investment in carnivory.

K, 26–70% Ca, and 34% for Mg. In this comparison, *A. vesiculosa* always reached the highest values for all nutrients.

Discussion

This study has shown relatively low values of tissue N and P content in different organ types in five aquatic rootless carnivorous plant species grown in culture, as compared to the most literature data for shoots of field-grown aquatic plants, while K, Ca, and Mg content was comparable (Table 1; cf. Adamec, 2008a; Dykyjová, 1979; Kamiński, 1987; Kosiba, 1992a). In all five aquatic carnivorous plant species of both genera, tissue nutrient contents usually differ significantly among traps, photosynthetic and carnivorous shoots. Except for the values of Ca and Mg contents, tissue N, P, and K contents were consistently higher in traps than those in photosynthetic shoots in *Aldrovanda* and two *Utricularia* species with monomorphic shoots; the same was found in *U. australis* (Adamec, 2008a). On the other hand, in *U. stygia* and *U. intermedia* with dimorphic shoots, tissue N, P, and K content was, significantly, the highest in photosynthetic shoots, while the lowest in carnivorous

shoots without traps. This relationship may be associated with the situation that in these species the function of carnivorous shoots is limited mainly to bearing the traps and transport functions (Adamec, 2007). Within the five species examined here and in *U. australis* (Adamec, 2008a), tissue K content was always significantly and markedly higher in traps (total range of 2.3–8.7%) than in shoots. Such a high tissue K content in *Utricularia* traps (3.7–8.7%) indicates that a relatively high K^+ concentration could occur in quadrid glands (Yang et al., 2009) which occupy a great proportion of the trap volume (e.g., Juniper et al., 1989).

As follows from the data above (Table 2), aquatic carnivorous plants invest, theoretically, about 19–78% of their total N, P, and K amount to mature traps (in monomorphic shoots) or carnivorous shoots with traps (in dimorphic shoots), as mineral cost of carnivory. This proportion is relatively high for N, P, and K in the species with monomorphic shoots. Traps and/or intact carnivorous shoots in aquatic carnivorous plants represent not only great losses of photosynthetic production (i.e., photosynthetic cost) but have also, simultaneously, great respiration demands (60–68% of the total plant respiration in three *Utricularia* species as energetic cost; Adamec, 2006, 2007). Besides this expenditure at the cost of struc-

tures (38–63% of total plant biomass; Table 2), they also represent a considerable mineral cost of macronutrients such as N, P, K, Ca, and Mg. Even though it can be assumed from limited studies (Adamec, 2000, 2008a) that a great proportion of trap N and P is re-utilized from senescent traps and carnivorous shoots, a part of N and P and all K, Ca, and Mg are lost in these senescent organs. Aquatic carnivorous plants with linear shoots usually grow very rapidly (Friday, 1989; Adamec, 2000, 2008b; Adamec and Kovářová, 2006) but the decomposition of basal shoot segments with traps can be no less rapid.

In this respect, for the ecological mineral benefit to prevail over the ecological mineral cost in aquatic carnivorous plants, three main associated ecophysiological processes should be optimized: the traps should capture as great a prey biomass as possible (i.e., high capture efficiency), they must efficiently take up growth-limiting mineral nutrients (N, P, K) from prey (i.e., high uptake efficiency), and they have to minimize the N and P losses in senescent traps and carnivorous shoots (i.e., high reutilization efficiency). As aquatic carnivorous plants evolved mainly in mineral-poor waters, it is probable that these mineral cost-benefit relationships always represented principal adaptive traits in the course of the evolution of aquatic carnivorous plants, i.e., a trend to maximize mineral nutrient uptake from prey per minimal mineral losses (N, P) invested into carnivory. The concept of mineral cost-benefit relationships does not deny the classic concept of ecological cost-benefit relationships of carnivory proposed by Givnish et al. (1984) for terrestrial carnivorous plants, which claims increased photosynthetic production as the main ecological benefit of carnivory. Yet, as increased photosynthetic rate has not been proven in aquatic carnivorous plants (Adamec, 2008b), it is possible to consider that the mineral concept applies to aquatic carnivorous plants whereas the photosynthetic one rather holds true for slowly growing terrestrial carnivorous plants (Farnsworth and Ellison, 2008).

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