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Dark respiration of leaves and traps of terrestrial carnivorous plants: are there greater energetic costs in traps?

Communication

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Abstract: In this study, O_2-based dark respiration rate (R_D) in leaf and trap cuttings was compared in 9 terrestrial carnivorous plant species of 5 genera to decide whether traps represent a greater energetic (maintanence) cost than leaves or photosynthetic parts of traps. R_D values of cut strips of traps or leaves of terrestrial carnivorous plants submerged in water ranged between 2.2 and 8.4 nmol g^{-1} s^{-1} (per unit dry weight) in pitcher traps of the genera *Sarracenia*, *Nepenthes*, and *Cephalotus*, while between 7.2 and 25 nmol g^{-1}_{DW} s^{-1} in fly-paper or snapping traps or leaves of *Dionaea* and *Drosera*. No clear relationship between R_D values of traps (or pitcher walls) and leaves (or pitcher wings or petioles) was found. However, RD values of separated *Drosera prolifera* tentacles exceeded those of leaf lamina 7.3 times.

Keywords: Sarracenia • Nepenthes • Cephalotus • Dionaea • Drosera • Aerobic respiration • Metabolic costs • Trap specialization

1. Introduction

On the ecophysiological level, the rate of aerobic dark respiration (R_D) of a plant organ is considered a measure of the intensity of metabolism and physiological functions of the organ. Such a concept is accepted also for carnivorous plants [e.g., 1,2]. Carnivorous plants represent an ecological, functional plant group comprising about 650 species in around 16 genera for which the capture of animal prey by use of specialised traps of foliar origin is typical. Nutrients are absorbed from prey carcasses, and utilized for plant growth and development [3]. [1] supplemented the classic theory from [4] on cost-benefit relationships of carnivory and hypothesised that carnivorous plants invest a greater energetic (metabolic) cost in its traps as an increased R_D but exhibit a reduced photosynthetic rate (P_N) comparatively to leaves as a photosynthetic cost. A great photosynthetic cost of carnivory was found in traps of seven species of aquatic *Utricularia* [1,2] which

are highly specialized organs entirely separated from their leaves. Similarly, trap R_D per unit dry weight (DW) was 10% higher than foliar R_D in *U. macrorhiza* [1] and even 1.9-3.3 times higher in six aquatic *Utricularia* species [2] so that the proportion of trap R_D to the total plant respiration amounted to 60-68% in three aquatic *Utricularia* species [2,5].

Pitcher-like traps in terrestrial carnivorous plants of the genera *Darlingtonia, Sarracenia,* and *Nepenthes* function as photosynthetic organs and traps simultaneously [e.g., 6-8] but there is a great shortage of data on their R_D. Although [7] demonstrated a crucial difference in P_N between pitcher traps and leaf laminae in two *Nepenthes* species (trap P_N was zero), the difference in R_D between the traps and laminae was ambiguous. Similarly, no significant difference in R_D was found between *Dionaea muscipula* traps and petioles and between *Sarracenia purpurea* pitcher wings and walls [9]. Yet, due to relatively very low maximum P_N (P_{Nmax}) in leaves or traps of terrestrial carnivorous plants,

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the R_D:P_{Nmax} ratio (as an expression of energetic cost of leaves; [10]) in carnivorous plant leaves is usually very high and values between 10-162% (mean about 40-60%) have been reported for various species [2,7,9,10] whereas these values are on average only about 8-17% in non-carnivorous plants [10,11]. It has recently been confirmed at least in some terrestrial carnivorous plant genera (*Sarracenia*, *Nepenthes*; [8,12]) that feeding on prey leads to a significant increase in biomass-based P_N but R_D in other species was unchanged [11,13].

The aim of this study was to compare O_2-based R_D in leaf and trap cuttings in 9 terrestrial carnivorous plant species of 5 genera and, thus, to decide whether traps of carnivorous plants represent a greater energetic (maintenance) cost than leaves or photosynthetic parts of traps.

2. Experimental Procedures

Experimental plants of *Sarracenia psittacina, S. rubra, S. minor, Nepenthes ventricosa, Cephalotus follicularis, Dionaea muscipula,* and *Drosera capensis* were grown in plastic pots in a mixture of peat and sand in a naturally-lit shaded greenhouse (for details see [9,14,15]). *Drosera prolifera* was grown in a shaded terrarium at a high relative air humidity, while *S. purpurea* ssp. *purpurea* was grown outdoors [10]. All plant species used except *S. purpurea* can be considered shade acclimated. Plants of *N. ventricosa* and *C. follicularis* obtained from a tissue culture (at least one year before) were young, their rosette diameter was only about 6-9 cm, and their pitchers were only 1.5-2.5 cm high. The other plant species were adult. All measurements were carried out during 30 May-4 July 2006.

Fully developed, adult pitchers or leaves were used for aerobic R_D measurements. In all *Sarracenia* species, about 1-1.5 cm^2 of pitcher walls and pitcher wings were cut using a razor blade from adjacent parts of pitchers about 3-18 cm below the peristome, *i.e.*, in the silver-like zone with bristles and glands (see [3]). The pitcher lid and peristome were removed from *N. ventricosa* and *C. follicularis* experimental pitchers before R_D measurement. In these species as well as in *Dionaea muscipula, Drosera capensis,* and *D. prolifera*, about 0.5-1 cm^2 of the leaf lamina or an adjacent part of the petiole were used for a single R_D measurement. In *D. capensis*, leaf lamina with intact tentacles were used together with petioles, while excised tentacles (about 50 tentacles, *c.a.* 2 mg fresh weight, FW) and leaf lamina without tentacles were used in *D. prolifera*. It may be assumed that the tentacles contributed about 4-5% to the whole leaf FW. The plant material for single R_D measurements originated from different plants. Before R_D measurements, the plant material of pitchers and leaves (petioles) was sliced to strips about 2.5-3 mm wide to enable a better oxygen exchange between the material and the solution used. It was demonstrated on preliminary samples that infiltration of these strips by the solution using under-pressure had no influence on the measured R_D. R_D was measured in a solution of 0.1 mM KCl and 0.05 mM CaCl$_2$ (80-90% O_2 saturation) in a 5-ml stirred chamber (kept at 22.0±0.1°C). A Clark-type oxygen sensor and a pen recorder (for details see [16]) was used. Before R_D measurements, the plant material was kept in dim daily light for 10-30 min. After R_D had been measured in darkness for about 15 min, FW was estimated, while DW (80°C) was estimated in pooled samples. FW of samples ranged from 16-120 mg. All measurements were repeated 6 times on different plant material. R_D is expressed in nmol O_2 g$^{-1}_{DW}$ s^{-1}. Means ±1.SE intervals are shown. Significant differences between pitcher walls (or traps or tentacles) and pitcher wings (or petioles or leaf lamina) were evaluated by a two-tailed t-test.

Species	Trap or tentacles		Pitcher wing or leaf or petiole	
	DW (% FW)	Respiration rate	DW (% FW)	Respiration rate
Sarracenia psittacina	20.6	2.40±0.49[a]	25.4	2.28±0.25[a]
Sarracenia rubra	24.5	4.98±0.41[a]	20.4	5.57±0.20[a]
Sarracenia minor	25.2	3.76±0.25[a]	22.8	4.79±0.27[b]
Sarracenia purpurea	18.4	8.38±0.32[a]	19.4	5.81±0.62[b]
Nepenthes ventricosa	6.1	8.20±1.47[a]	9.6	5.86±0.93[a]
Cephalotus follicul.	8.9	2.22±0.26[a]	11.5	4.26±0.25[b]
Dionaea muscipula	12.6	14.2±2.0[a]	12.9	12.3±1.2[a]
Drosera capensis	16.5	20.8±0.9[a]	12.1	24.9±0.4[b]
Drosera prolifera	--	52.0±7.5[a]	17.7	7.16±0.70[b]
	tentacles	(n=4)	leaf lamina	(n=4)

Table 1. Oxygen-based dark respiration rates (in nmol g$^{-1}_{DW}$ s^{-1}) of traps with glands and of pitcher wings or petioles of the same leaves of terrestrial carnivorous plants at 22.0±0.1°C. Mean ±1.SE is shown when possible; n=6. The same letters within the rows denote no statistically significant difference at P<0.05. The percentage of DW in FW is also shown.

3. Results

Out of 4 *Sarracenia* species used, R_D of *S. psittacina* and *S. rubra* in pitcher walls as a part of traps was not significantly different from R_D values estimated in adjacent pitcher wings (Table 1). In *S. minor* pitcher wings and in *S. purpurea* pitcher walls, DW-based R_D values were significantly higher than those in the opposite organ part. Slightly higher R_D in *N. ventricosa* pitchers did not differ significantly from that in leaves, while a significantly higher R_D (4.26 ± 0.25 nmol g^{-1}_{DW} s^{-1}) was found in *C. follicularis* leaves as compared to pitchers (2.22 ± 0.26 nmol g^{-1}_{DW} s^{-1}). R_D of the snapping trap lobes of *Dionaea muscipula* did not differ significantly from that of petioles. In *D. capensis,* DW-based R_D of petioles was by about 20% higher than that of leaves with tentacles (Table 1) but the FW-based R_D values were opposite and significantly different (data not shown). However, R_D of separated *D. prolifera* tentacles was 7.3 times higher than that of the leaf lamina without tentacles, suggesting a very high metabolic activity in tentacles.

4. Discussion

All traps of carnivorous plants, regardless of their structure and function, contain tissues in the form of secretory and absorptive glands [3] due to which the traps could be metabolically (R_D) more active per unit biomass than the adjacent foliar tissues. However, it is evident that the energetic, maintenance demand or cost of traps in comparison with leaves greatly depends on the type of the trap: on the way of its operation (active or passive trapping) and on its specialisation and complexity. In very specialised *Utricularia* traps possessing a peculiar mutant in a mitochondrial cytochrom *c* oxidase, which allows a greater energetic power [17] serving for intensive water pumping, R_D values are much greater than those of leaves [2], whereas R_D values in related *Genlisea* traps without any active water flow are relatively low [16]. Similarly, in relatively unspecialised pitcher traps, the difference in R_D between traps and leaves (or pitcher walls and wings) is rather small or ambiguous [7,10]. The O_2-based R_D values found here confirmed this relationship (Table 1). Moreover, the same ambiguous relationship between R_D of traps and petioles was found in *Droseraceae* leaves - in *Dionaea muscipula* and *Drosera capensis* (cf. also [10]). However, the many times greater R_D of separated *D. prolifera* tentacles in comparison with that of leaf lamina proves a very high metabolic and physiological activity of tentacles

comprising enzyme secretion, nutrient absorption, electrical irritability, and bending [3,18]. It indicates that the discrete magnitude of R_D of whole leaves containing traps always depends on the biomass proportion of these highly metabolically active trap structures to the whole leaf biomass. In this way, the magnitude of R_D of traps is generally genus specific. Yet, the highest R_D of *S. purpurea* traps among all *Sarracenia* species might be caused by sun acclimation in this species.

In summary, the O_2-based R_D values of cut strips of traps or leaves of terrestrial carnivorous plants submerged in water ranged between 2.2 and 8.4 nmol g^{-1}_{DW} s^{-1} in pitcher traps of the genera *Sarracenia, Nepenthes,* and *Cephalotus*, while between 7.2 and 25 nmol g^{-1}_{DW} s^{-1} in fly-paper or snapping traps or leaves of *Dionaea* and *Drosera* (Table 1). These values are comparable with those measured as CO_2 exchange in the air in intact or excised organs of the same or similar carnivorous plant species and also in leaves of two European *Pinguicula* species (total range 6-45 nmol g^{-1}_{DW} s^{-1}; [7,10,12]). Generally, mean R_D values (per unit DW) in leaves and traps of terrestrial carnivorous plants are about by one-third lower than those reported by [19] for leaves of 16 non-carnivorous plant species (mean about 35, range 15–100 nmol CO_2 g^{-1}_{DW} s^{-1}). The mildly lower R_D values in terrestrial carnivorous plants however are associated with low P_{Nmax} values in their leaves or traps, which are (per unit DW or leaf area) 2-4 times lower than those in leaves of non-carnivorous plants [10,20]. Therefore, R_D:P_{Nmax} ratio is usually very high in carnivorous plant leaves or traps [9]. The low P_{Nmax} values reflect the slow growth of terrestrial carnivorous plants (*sensu* [21]).

In conclusion, it is generally accepted that the main ecophysiological benefit of carnivory in carnivorous plants is based on the uptake of growth-limiting mineral nutrients N and P from prey; in several species, stimulation of photosynthesis as a photosynthetic benefit also takes place [6,8,13]. It is possible to assume that carnivorous plants sought to minimize the cost: benefit relationships during their evolution, *i.e.*, to keep the ratio: (energetic + photosynthetic costs of traps) : (nutritional benefit of prey capture + photosynthetic benefit of leaves) as low as possible. In terrestrial carnivorous plants, which grow relatively slowly and, therefore, do not need high P_{Nmax} values, the relatively high energetic and photosynthetic costs may not be so important if they are counterbalanced by a sufficient nutritional benefit of prey capture.

Acknowledgements

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