

# 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<sub>2</sub>-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 (maintenance) 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<sup>-1</sup> s<sup>-1</sup> (per unit dry weight) in pitcher traps of the genera *Sarracenia*, *Nepenthes*, and *Cephalotus*, while between 7.2 and 25 nmol g<sup>-1</sup> DW s<sup>-1</sup> 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

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## 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<sup>2</sup> 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<sup>2</sup> 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<sub>2</sub> (80-90% O<sub>2</sub> 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<sub>2</sub> g<sup>-1</sup> DW s<sup>-1</sup>. 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       |
| <i>Sarracenia psittacina</i> | 20.6              | 2.40±0.49 <sup>a</sup> | 25.4                            | 2.28±0.25 <sup>a</sup> |
| <i>Sarracenia rubra</i>      | 24.5              | 4.98±0.41 <sup>a</sup> | 20.4                            | 5.57±0.20 <sup>a</sup> |
| <i>Sarracenia minor</i>      | 25.2              | 3.76±0.25 <sup>a</sup> | 22.8                            | 4.79±0.27 <sup>b</sup> |
| <i>Sarracenia purpurea</i>   | 18.4              | 8.38±0.32 <sup>a</sup> | 19.4                            | 5.81±0.62 <sup>b</sup> |
| <i>Nepenthes ventricosa</i>  | 6.1               | 8.20±1.47 <sup>a</sup> | 9.6                             | 5.86±0.93 <sup>a</sup> |
| <i>Cephalotus follicul.</i>  | 8.9               | 2.22±0.26 <sup>a</sup> | 11.5                            | 4.26±0.25 <sup>b</sup> |
| <i>Dionaea muscipula</i>     | 12.6              | 14.2±2.0 <sup>a</sup>  | 12.9                            | 12.3±1.2 <sup>a</sup>  |
| <i>Drosera capensis</i>      | 16.5              | 20.8±0.9 <sup>a</sup>  | 12.1                            | 24.9±0.4 <sup>b</sup>  |
| <i>Drosera prolifera</i>     | --                | 52.0±7.5 <sup>a</sup>  | 17.7                            | 7.16±0.70 <sup>b</sup> |
|                              | tentacles         | (n=4)                  | leaf lamina                     | (n=4)                  |

**Table 1.** Oxygen-based dark respiration rates (in nmol g<sup>-1</sup> DW s<sup>-1</sup>) 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  $R_D$  ( $4.26 \pm 0.25 \text{ nmol g}^{-1}_{\text{DW}} \text{ s}^{-1}$ ) was found in *C. follicularis* leaves as compared to pitchers ( $2.22 \pm 0.26 \text{ nmol g}^{-1}_{\text{DW}} \text{ s}^{-1}$ ).  $R_D$  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  $\text{O}_2$ -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  $\text{O}_2$ -based  $R_D$  values of cut strips of traps or leaves of terrestrial carnivorous plants submerged in water ranged between 2.2 and  $8.4 \text{ nmol g}^{-1}_{\text{DW}} \text{ s}^{-1}$  in pitcher traps of the genera *Sarracenia*, *Nepenthes*, and *Cephalotus*, while between 7.2 and  $25 \text{ nmol g}^{-1}_{\text{DW}} \text{ s}^{-1}$  in fly-paper or snapping traps or leaves of *Dionaea* and *Drosera* (Table 1). These values are comparable with those measured as  $\text{CO}_2$  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  $\text{nmol g}^{-1}_{\text{DW}} \text{ s}^{-1}$ ; [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  $\text{nmol CO}_2 \text{ g}^{-1}_{\text{DW}} \text{ s}^{-1}$ ). The mildly lower  $R_D$  values in terrestrial carnivorous plants however are associated with low  $P_{\text{Nmax}}$  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,  $R_D \cdot P_{\text{Nmax}}$  ratio is usually very high in carnivorous plant leaves or traps [9]. The low  $P_{\text{Nmax}}$  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  $P_{\text{Nmax}}$  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.

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