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Chapter IX

Ecophysiological Look at Organ Respiration in Carnivorous Plants: A Review

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Abstract

On the ecophysiological level, the magnitude 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. In this minireview, properties of R_D are reviewed in different types of organs of carnivorous plants from a functional point of view. Although net photosynthetic rate (P_N) in leaves or traps of terrestrial carnivorous plants is usually several times lower than that in leaves of vascular non-carnivorous plants, R_D in carnivorous plant leaves is relatively high and reaches on average 48 % of P_{Nmax} representing the high metabolic (energetic) cost of carnivory. The metabolic cost of carnivory is markedly high in traps of aquatic carnivorous *Utricularia* species; the traps are structurally quite separate from photosynthetic leaves. In six species, trap R_D was 75-200 % greater than that in leaves but foliar P_N exceeded that in traps 7-10 times. This reflects high metabolic activity of *Utricularia* traps associated with pumping ions and water through the trap walls. However,

it has not yet been explained how the internal trap structures (glands taking part in prey digestion, nutrient absorption, and pumping water) provide the ATP for their demanding functions when complete anoxia occurs in the trap fluid.

R_D values of roots ($1.6\text{--}5.6 \text{ nmol g}^{-1} \text{ FW s}^{-1}$) as well as water exudation rates of five carnivorous plant species were comparable with those reported in non-carnivorous plants or even higher. A high proportion of cyanide-resistant respiration (65–89 %) was found in the roots. R_D values of turions (winter buds) of some aquatic carnivorous plant species of the genera *Aldrovanda* and *Utricularia* were about 1.5–4 times lower (on FW basis) than those reported in growing shoots/leaves of these or other aquatic plant species. Contrary to true dormant turions, R_D of non-dormant winter shoot apices of *Aldrovanda* and *Utricularia* was comparable to that in aquatic plant shoots/leaves.

Introduction

On the ecophysiological level, the magnitude 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., Adamec 2005, 2006). Carnivorous plants represent an ecological, functional plant group comprising about 650 species of about 16 genera for which it is typical that they capture animal prey by their specialised traps of foliar origin, absorb nutrients from prey carcasses, and utilize them for their growth and development (Juniper et al. 1989). As compared to other processes like rapid movements, prey digestion, enzyme secretion, or nutrient uptake in carnivorous plants, which have always attracted the curiosity of botanists (Juniper et al. 1989, Adamec 1997a), the study of respiration of carnivorous plants has been neglected up to now. Knight (1992) supplemented the classic theory from Givnish et al. (1984) on cost-benefit relationships of carnivory and hypothesised that carnivorous plants invest a greater metabolic (energetic) cost in its traps as an increased R_D but reduced photosynthetic rate (P_N) comparatively to leaves. So far, only several respiration studies have been published for carnivorous plants (see Ellison and Gotelli 2009). They include comparisons of R_D of traps and leaves (Knight 1992; Méndez and Karlsson 1999; Adamec 2006; Pavlovič et al. 2007; Hájek and Adamec 2009) and particulars on R_D of *Utricularia* and *Genlisea* traps (Adamec 2007b), carnivorous plant roots (Adamec 2005), and overwintering buds (turions;

Adamec 2003). In this minireview, properties of R_D in different types of organs of carnivorous plants are reviewed from a functional point of view.

Dark Respiration of Traps and Leaves

As hypothesized by Knight (1992) traps of carnivorous plants as highly specialized organs have higher R_D than leaves/shoots and, simultaneously, due to their lower P_N , represent a great photosynthetic cost. Generally, as compared to leaves of non-carnivorous plants, in which the $R_D:P_{Nmax}$ ratio (as an expression of metabolic cost of leaves) is on average only about 8-17 % (Givnish 1988; Wright et al. 2004), the ratio in carnivorous plant traps is usually much higher and values between 10-162 % (mean about 40-60 %, i.e. 15-25 $\text{nmol g}^{-1}_{\text{DW}} \text{s}^{-1}$, total range 6-45 $\text{nmol g}^{-1}_{\text{DW}} \text{s}^{-1}$) have been reported for various species (Méndez and Karlsson 1999; Adamec 2006; Pavlovič et al. 2007; Hájek and Adamec 2009). Although this ratio is surprisingly high in highly specialized aquatic *Utricularia* traps (50-140 %, Adamec 2006), there are no indications that aquatic carnivorous species differ distinctly from terrestrial ones in this parameter (cf. Hájek and Adamec 2009). Rather, very low P_{Nmax} values in *Utricularia* traps are responsible for this ratio. However, even in spite of the scarcity of data, due to highly specialized traps in aquatic carnivorous species, it is obvious that traps of aquatic species represent relatively, per unit DW, much greater metabolic cost (as the trap:leaf R_D ratio) than that of terrestrial species (though it is not possible to compare the proportion of trap R_D to total plant R_D due to a quite different proportion of trap DW in various taxa). As shown by Pavlovič et al. (2007) for two *Nepenthes* species and by Hájek and Adamec (2009) for *Dionaea muscipula* and *Sarracenia purpurea* no consistent difference occurred in DW-based R_D between traps and leaves. However, fresh-weight-based R_D of excised, physiologically highly active tentacles of *Drosera prolifera* was 7.3 times higher than that of the leaf laminae without tentacles (Adamec, unpubl.). Similarly, DW-based trap R_D was by 10 % higher than foliar R_D in *U. macrorhiza* (Knight 1992) and even 1.9-3.3 times higher in six aquatic *Utricularia* species (Adamec 2006) so that the proportion of trap R_D to the total plant respiration amounted to 60-68 % in three aquatic *Utricularia* species (Adamec 2006, 2007a). As it follows from very limited data R_D was changed due to prey addition neither in *Pinguicula vulgaris* leaves (Méndez and Karlsson 1999) nor in two aquatic species (Adamec 2008a) although

P_{Nmax} could be stimulated by this treatment in several species (Adamec 2008a; Farnsworth and Ellison 2008). As carnivorous plants can also take up organic substances from prey carcasses (Juniper et al. 1989, Adamec 1997a) new research should determine generally whether prey addition changes R_D in leaves and traps and the metabolic cost of carnivory, as a possible reason for the increased organ growth.

Particulars of Respiration of *Utricularia* and *Genlisea* Traps

About 50 *Utricularia* (Lentibulariaceae) species are rootless aquatic or amphibian plants which grow in standing, nutrient-poor shallow wetlands in waters with larger concentrations of humic acids and tannins (Juniper et al. 1989). *Utricularia* species capture aquatic prey, such as small crustaceans, mites, rotifers, and protozoa, in their traps (Harms 1999; Jobson and Morris 2001; Richards 2001). Moreover, diverse communities of microorganisms, mainly bacteria, algae, protozoa and rotifers, live inside traps as commensals (Jobson and Morris 2001; Richards 2001). The trap is a water-filled utricle 1-5 mm long with a wall two cell layers thick and a variety of glands and trichomes on both surfaces (Juniper et al. 1989). After an irritation of trigger hairs situated close to the trap door, an organism is sucked in as a result of under-pressure maintained inside the trap (Sydenham and Findlay 1973). During about 30 min after firing, approx. 40 % of the trap water is pumped out and the trap is ready to fire again. Thus, as a consequence of firing, the trap is partly re-filled with the ambient water together with all solutes and particles.

Generally, *Utricularia* traps are physiologically very active organs. Their aerobic DW-based R_D values were 1.9-3.3 times higher (25-43 nmol O_2 g⁻¹ s⁻¹) than those of adjacent leaves/shoots (Adamec 2006). Ion and water pumping during the resetting of traps depended markedly on aerobic respiration as inhibitors such as KCN and NaN₃ prevented it when applied internally into traps; outer application was ineffective (Sydenham and Findlay 1975). However, Adamec (2007b) found consistently steady-state zero O_2 concentrations in the trap fluid of traps without prey in six aquatic *Utricularia* species regardless of whether the traps were intact or excised from the shoot or in light or darkness. Thus, under natural conditions, long periods of anoxia inside the traps can be interrupted by periods of 20-100 min after accidental trap firing when a measurable O_2 concentration occurs in the trap fluid. Therefore, captured organisms either die of O_2 deprivation within several

hours and are prey, or are able to tolerate anoxia and are commensals. The fact of the steady-state zero O_2 concentration suggests that internal glands of empty *Utricularia* traps have potentially a very high aerobic R_D when O_2 is available and that they are able to consume all O_2 inside the trap within 20-100 min (Adamec 2007b). It might be the only period when the internal trap structures respire aerobically. The comparison of the 'external' aerobic R_D of *U. reflexa* traps (cut-off traps; $1.03 \pm 0.07 \text{ nmol g}^{-1}_{FW} \text{ s}^{-1}$) with the 'total' aerobic R_D (halved traps; $1.31 \pm 0.07 \text{ nmol g}^{-1}_{FW} \text{ s}^{-1}$) further confirmed that the trap fluid is very isolated from the ambient water outside the traps and that anoxia in the trap fluid is not transferred outdoors. The difference between the 'total' and 'external' aerobic R_D could be attributed to 'internal' aerobic R_D of internal trap structures, mainly glands, and was consistent with the rate of decline of O_2 concentration in the trap fluid measured directly inside the traps.

However, it does not follow from the above facts how the traps really obtain their ATP energy for filling their demanding physiological functions. As there is often a low or even zero O_2 concentration in the ambient water around traps (Guisande et al. 2000, 2004; Adamec 2007a) the period of aerobic respiration after a firing could be markedly shorter than the resetting time needed. It is probable then that the internal glands obtain their metabolic energy from anaerobic fermentation. Thus, further research should determine whether products of anaerobic fermentation (e.g., ethanol, propionic acid) are produced in traps under anoxia. This conclusion does not contradict the hypothesis and findings of Jobson et al. (2004), who suggest a link between faster reaction kinetics of *Utricularia* traps and mutations occurring in the mitochondrial respiratory chain enzyme cytochrome *c* oxidase. Laakkonen et al. (2006) further hypothesize decoupling of mitochondrial proton pumping from electron transfer, which could be a rich source of ATP energy after trap firing under anoxic conditions. Such decoupling would permit traps to optimize power output during times of need. It should be added that traps with digesting prey can have much greater energetic demand than empty traps and that R_D of mainly heterotrophic trap commensals should also be taken into account in all respiration studies in *Utricularia* traps.

Genlisea (Lentibulariaceae) grows in anoxic wet substrates and forms short stems with a rosette of small green leaves and tubular subterranean traps of foliar origin (Juniper et al. 1989). The inverted Y-shaped traps are 3-12 cm long and about 1 mm in diameter. The hollow traps function as 'eel traps'. Digestive glands are abundant in the cavity of the trap. *Genlisea* traps capture fine soil organisms (bacteria, algae, protozoans, nematodes, rotifers, annelids,

crustaceans, and mites (Barthlott et al. 1998; Plachno et al. 2005; Plachno and Wołowski, 2008). The traps are probably passive (Plachno et al. 2008). This explains that, unlike *Utricularia* traps, aerobic R_D in traps of three *Genlisea* species was very low ($0.38\text{--}1.14 \mu\text{mol g}^{-1} \text{FW s}^{-1}$) and quite insensitive to either 0.5 mM KCN or 0.2 mM NaN_3 (Adamec 2005). A high proportion of cyanide-resistant respiration (74-87 % of the total R_D) was found in all three species. Trap walls in *Genlisea* (around the vesicle and tubular neck) contain large air spaces connecting them with leaves. Although nearly-saturated O_2 concentrations occurred in the trap walls in *G. hispidula*, the O_2 concentration in the fluid in the central trap cavity in the vesicle and 2 mm below it was strictly zero (Adamec 2007b). This situation is exactly the same like in *Utricularia* traps: abundant digestive glands lining the central trap cavity are able to consume all O_2 diffusing inside the trap from the walls in spite of that the trap is not closed. Again, it is not clear how the digestive glands inside *Genlisea* traps respire under complete anoxia.

Respiration of Carnivorous Plant Roots

Roots of the majority of carnivorous plants grow in bog and fen soils which are usually wet or waterlogged, mostly acidic, and poor in available mineral nutrients (Juniper et al. 1989). A weakly developed root system is common for most species and the root:total biomass ratio lies only between 3.4-23 % (Adamec 1997a). Aerobic R_D values were between $1.6\text{--}5.6 \text{ nmol O}_2 \text{ g}^{-1} \text{FW s}^{-1}$ in apical root segments in seven carnivorous plant species (Adamec 2005). However, the rate of anaerobic fermentation in roots of two *Drosera* species was only 5-14 % of the aerobic R_D . Neither 0.5 mM KCN nor 0.2 mM NaN_3 influenced root R_D . In roots of five carnivorous species, the proportion of cyanide-resistant respiration was high and between 65-89 % of the total R_D value. Thus, the R_D values found in roots of carnivorous plants are comparable with those reported in roots of non-carnivorous plants in the literature or even higher. Generally, carnivorous plant roots appear to be physiologically very active and well adapted to endure permanent soil anoxia, mainly due to oxygen diffusion through the root intercellulars (Adamec 2005).

Respiration of Turions

Turions are vegetative dormant storage organs produced by perennial aquatic plants. They are modified shoot apices and protect fragile plant shoots from freezing and decaying (Bartley and Spence 1987). Turions of free-floating aquatic carnivorous plants *Aldrovanda* and *Utricularia* spp. break their dormancy at the bottom of an aquatic habitat, but usually germinate at the water surface, in warmer water and at higher irradiance (Adamec 1999, 2003, 2008bBI). *Aldrovanda* turions break off the dying mother shoots, actively sink in autumn and rise in the spring, while *Utricularia* turions are dragged down by decaying shoots (Adamec 1999). The FW-based aerobic R_D of *Aldrovanda vesiculosa* turions at 20 °C ($0.74\text{--}1.5 \text{ nmol O}_2 \text{ g}^{-1}_{\text{FW}} \text{ s}^{-1}$) was rather low on an absolute scale and reached only about 27-55 % of that of growing shoots of the same species (cf. Adamec 1997b, 2003). It was only $0.22 \pm 0.02 \text{ nmol g}^{-1}_{\text{FW}} \text{ s}^{-1}$ at 4 °C (Q_{10} 2.78). No significant differences in R_D occurred between innate (autumn) and imposed dormancy (spring) or during two days of breaking imposed dormancy at 20 °C (Adamec 2003). However, the anaerobic fermentation rate of *Aldrovanda* turions was only 1.5-7 % of the aerobic R_D and was also constant during the breaking of imposed dormancy. Such a low ratio might reflect both low energy consumption in overwintered turions and their biochemical adaptation to anoxia, saving reserve sugars. It may be suggested that a spring temperature increase causes an increase of turion fermentation or R_D which is further responsible for the evolution of gas in turion lacunae and, thus, for turion rising.

In autumnal (dormant) turions of four aquatic carnivorous plant species (*A. vesiculosa*, *U. australis*, *U. ochroleuca*, *U. bremitii*), aerobic R_D values ranged from $0.36\text{--}0.71 \text{ nmol O}_2 \text{ g}^{-1}_{\text{FW}} \text{ s}^{-1}$ at 20 °C and, except for *U. bremitii*, increased by 11-114 % after overwintering (Adamec 2008b). These R_D values of dormant turions represented only 25-73 % of those found in photosynthetic shoots of the same species (cf. Adamec 2006). Thus, turions behave as typical storage, overwintering organs with low R_D . Respiration Q_{10} ranged from 1.75-2.55 in dormant turions and from 2.59-3.39 in non-dormant turions. Except for *Aldrovanda*, turion R_D was not reduced in 0.5 mM KCN (Adamec 2008b). In all turions, the proportion of cyanide-resistant respiration was high and between 50-90 % of the total R_D value. As very similar respiration characteristics were also found in turions of two non-carnivorous species, *Hydrocharis morsus-ranae* and *Caldesia parnassifolia* (Adamec 2008b), it may be concluded that respiration characteristics of turions are not dependent

on plant carnivory. However, contrary to true turions, R_D values in non-dormant winter apices both in Australian *Aldrovanda* populations and temperate *U. radiata* and subtropical *U. purpurea*, and in sprouting turions of temperate *Aldrovanda* were high (2.1 – 3.1 nmol O_2 g⁻¹ FW s⁻¹ at 20 °C; Adamec 2008b) and similar to those in aquatic plant leaves or shoots.

Conclusion

As follows from the review study of dark respiration has brought a substantial progress in understanding ecophysiological traits in carnivorous plants. As shown some organs of carnivorous plants (roots, *Utricularia* and *Genlisea* traps, turions) normally face strong hypoxia or anoxia but it is not clear how they do provide ATP energy to ensure their physiological functions under these conditions as their respiration characteristics have mainly been studied under aerobic conditions. R_D has been found to be a distinct criterion between the true, dormant turions and non-dormant winter apices in some aquatic carnivorous plant species.

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