# ECOPHYSIOLOGICAL LOOK AT PLANT CARNIVORY:
## *Why are plants carnivorous?*

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## 1. Introduction

About 650 species of vascular carnivorous (Latin: carnis – flesh, vorare – to swallow) plants occur throughout the world (e.g., Rice, 2006) out of the total of about 300,000 species of vascular plants. Carnivorous plants belong to 15-18 genera of 8-9 botanical families and 5 orders (Givnish, 1989; Juniper et al., 1989; Müller et al., 2004; Heubl et al., 2006; Porembski and Barthlott, 2006; Studnička, 2006). Due to many remarkable and striking morphological, anatomical, physiological, and ecological features, carnivorous plants have always attracted considerable interest of both researchers and gardeners. Nevertheless, the degree and extent of knowledge of the main disciplines studying this particular ecological functional plant group has always considerably lagged behind the study of non-carnivorous plants. However, similar to the dynamically growing knowledge of non-carnivorous plants, the study of carnivorous plants has developed very rapidly and progressively within the last decade, mainly due to the use of modern molecular taxonomic approaches. Also, modern ecophysiological research of carnivorous plants has progressed considerably within the last decade and has elucidated most of the particulars of carnivorous plants. Thus we are increasingly more able to discuss to what extent carnivorous plants are unique from or common with "normal" non-carnivorous plants.

The aim of this paper is to classify and review recent experimental results and concepts concerning plant carnivory from an ecophysiological point of view, with an emphasis on mineral nutrition, growth characteristics, and comparison of aquatic and terrestrial carnivorous plants. The latter two subjects have often been neglected in previous reviews (cf. Juniper et al., 1989). The present review is focused on mineral nutrition as it is believed that mineral nutrition represents the key processes and the main benefit of carnivory for these plants (Adamec, 1997a; Ellison and Gotelli, 2001). A new model of "nutritional" cost-benefit relationships is presented. However, there are several other remarkable ecological phenomena associated with carnivory, e.g., prey-pollinator conflict (Zamora, 1999), prey attraction (Givnish, 1989), prey selectivity (Harms, 1999), competition between carnivorous and non-carnivorous plants (Brewer, 1999a,b), and relationships within inquiline communities in pitcher traps (Gray et al. 2006). Most of these phenomena were thoroughly reviewed by Ellison et al. (2003) and will not be mentioned in this study.

The present review follows from previous review publications in this field. Undoubtedly, Darwin (1875) was the first who summarized multilateral research on carnivorous plants, even though the main focus of his book was aimed at his studying the irritability of *Drosera* tentacles. He was the first to prove digestion of prey and to reveal that carnivorous plants showed enhanced growth if fed on insects and/or animal proteins. Darwin's book greatly influenced and inspired several generations of botanists and physiologists studying carnivorous plants. About 70 years after Darwin, the knowledge of carnivorous plants, based on literature items, were comprehensively reviewed in a monograph by Lloyd (1942). Physiological investigations on carnivorous plants, focusing on mineral and organic nutrition, trap excitation and movement, and digestive enzyme secretion were reviewed by Lüttge (1983). Evolution and ecological cost-benefit relationships of carnivorous plants were discussed thoroughly by Givnish (1989) in his review. Carnivorous plant biology, with an emphasis on cytology, anatomy, biochemistry, and physiology, was reviewed in detail in an excellent monograph by Juniper et al. (1989). This review includes all literature sources published before 1987-1988, and serves as a reference list of literature. In the decade after this monograph appeared, the mineral nutrition of carnivorous plants has been studied intensively. The subjects of mineral and organic nutrition of carnivorous plants as key ecophysiological processes associated with carnivory were classified and thoroughly reviewed by Adamec (1997a), who separately analyzed processes in field- and greenhouse-grown plants and also in terrestrial and aquatic carnivorous plants. Modern trends in studying carnivorous plants with an emphasis on phylogenetic diversity and cost-benefit relationships were reviewed in a well-arranged way by Ellison and Gotelli (2001). Selected ecological phenomena and processes associated with carnivory were reviewed in details by Ellison et al. (2003). Proceedings of a special Session on "Biology of Carnivorous Plants," at the International Botanical Congress held in Vienna, Austria, in 2005, were published in a special issue of Plant Biology 8(6) in 2006 (for comments see Porembski and Barthlott, 2006). In this special issue, Ellison (2006) reviewed ecophysiological subjects of nutrient limitations in carnivorous plants and identified modern directions for this research. Finally, Guisande et al. (2007) have recently published a detailed review on the bladderwort (*Utricularia*) genus which includes also some ecophysiological points.

## 2. Plant carnivorous syndrome

All plants considered carnivorous have to fulfill several criteria to separate them from other ecological plant groups (e.g. saprophytes). Nevertheless, due to a great diversity of ecological and functional plant traits, these criteria are still partly ambiguous (cf. Juniper et al., 1989; Adamec, 1997a). Thus, what is really *crucial* for a working definition of "plant carnivory"? Considering that the main ecophysiological benefit and consequence of carnivory is the uptake of growth-limiting mineral nutrients from prey, the criteria for the carnivorous syndrome (i.e. cluster of characters) may be as follows: a) capturing or trapping prey in specialized traps, b) absorption of metabolites (nutrients) from killed prey, and c) utilization of these metabolites for plant growth and development (Lloyd, 1942; Givnish 1989; Juniper et al., 1989; Adamec, 1997a). As all plants are able to absorb organic substances from soil (e.g. from dead animals), the criterion of capturing prey in traps, which actively kill prey, separates carnivorous from saprophytic plants. Moreover, Juniper et al. (1989) and many later authors state two other criteria such as prey attraction and digestion. However, on the basis of recent knowledge of this issue, it is possible to conclude that these additional criteria are not indispensable for functioning of carnivorous plants. First, the ability to attract prey has only been studied and confirmed in a part of carnivorous plants yet and it is not clear whether or not it occurs in very abundant genera of carnivorous plants such as *Utricularia* and *Genlisea* (Givnish, 1989; Guisande et al., 2007; Płachno et al., unpubl.). Moreover, the study on north European *Pinguicula* species (Karlsson et al., 1987) did not reveal prey attraction in *P. alpina*, in contrast with other species, without the plant being limited by prey capture. Second, it is generally accepted that carnivorous plants can also digest prey without secreting their own hydrolytic digestive enzymes in traps, relying only on enzyme secretion by trap commensals (e.g. Givnish., 1989; Jaffe et al., 1992; Butler et al., 2008). Thus, these two additional criteria – prey attraction and digestion – may rather be considered technical details which can only improve the efficiency of carnivory but are not indispensable for carnivory as such. In an analogy with parasitic plants (holoparasites and hemiparasites), Joel (2002) proposed the term "holocarnivory" for carnivorous plants secreting their own digestive enzymes (e.g. *Dionaea, Drosera, Drosophyllum, Pinguicula, Nepenthes*) and "hemicarnivory" for those plants which do not (e.g. *Brocchinia*, *Roridula*).

However, the diversity of ecological relationships concerning prey digestion is evidently wider and an additional classification can be based on the way by use of which carnivorous plants gain nutrients from prey, regardless of secretion of own enzymes. All carnivorous plants except for *Roridula* can gain nutrients from prey carcasses more-or-less *directly* and such a type of carnivory can be termed as "direct". Two *Roridula* species, however, capture prolific prey but they usually do not digest it. The captured prey are grazed by kleptoparasitic hemipteran bugs *Pameridea* which are found only on the *Roridula* plants and which defecate on its surface; the plants absorb nutrients through specialized cuticular gaps (Ellis and Midgley, 1996; Midgley and Stock, 1998; Anderson et al. 2003; Anderson 2005). Thus, mineral nutrients from prey are gained *indirectly*, through excrements of the bugs as mediator, and this type of carnivory can be termed as "indirect".

Discussing the carnivorous syndrome, one can make a physiological look at plant carnivory and question to what extent carnivorous plants are physiologically unique within the plant kingdom. In line with Juniper et al. (1989, p. 10-11), it is possible to point out five physiological key processes which are typical and common for plant carnivory: a) rapid movements of traps; b) their electrophysiological regulation; c) hydrolytic enzyme secretion; d) foliar uptake of nutrients; e) stimulation of root nutrient uptake by foliar nutrient uptake. Yet, *all* these *individual* processes can also occur in non-carnivorous plants and, therefore, they are not confined only to carnivorous plants and are not unique in this plant group. In carnivorous plants, however, they occur very often and together, forming a coordinated functional unit within which one process is firmly coupled with another one.

## 3. Ecological characteristics of terrestrial carnivorous plants and their habitats

The majority of terrestrial carnivorous plants grow in bog and fen soils in which they encounter persistent unfavourable conditions. The soils are usually wet or waterlogged, at least during the growing period. The only exception may be *Drosophyllum lusitanicum*, growing in dry sandy or rocky soils (Adlassnig et al., 2006), or hemicarnivorous epiphytes such as *Catopsis berteroniana*. The soils are mostly acid (pH 3-6; e.g. Roberts and Oosting, 1958; Chandler and Anderson, 1976a; Juniper et al., 1989, p. 21-22) but some are neutral or slightly basic (e.g. Schwintzer, 1978). They usually contain a high proportion of slowly decomposing organic matter (plant remnants). Due to waterlogging, the soils are partly (hypoxia) or entirely (anoxia) deprived of oxygen. Moreover, changing of anaerobic and aerobic conditions is also harmful (post-anoxic injury; Crawford, 1989, p. 105-129). In wet soils, decomposition of organic matter may lead to a high concentration of toxic $H_2S$ (or $S^{2-}$) and a low redox potential. When redox potentials are low, iron and manganese may solubilize and become toxic to plant roots, while some other microelements may become unavailable to plants (Crawford, 1989).

It is presumably the very low level of macronutrients available to plants which is the primary unfavourable ecological factor in these soils, that is overcome by carnivory (Lüttge, 1983; Juniper et al., 1989). However, there is a tremendous difference between the *available* and *total* macronutrient content in most bog and fen soils. For example, Roberts and Oosting (1958) reported very low available nutrient content in bog soils with *Dionaea* in North Carolina (in $mg.kg^{-1}$ dry weight, DW): $NH_4^+$, 2; $PO_4$, less than 2; K, 2; Mg, 1; Fe, 1. There was a complete lack of detectable $NO_3^-$, Ca, and Mn. However, the available nutrient content in more fertile fen soils can be one to two orders of magnitude higher (e.g. Schwintzer, 1978; Aldenius et al., 1983). In contrast, the following total N and P contents were found in bog soils inhabited by four Australian and New Zealand *Drosera* species (in $g.kg^{-1}$ DW): N, 0.46-2.5; P, 0.09-1.9 (data summarized by Chandler and Anderson, 1976a).

Normal functioning of carnivorous plant roots (uptake of nutrients and water) is dampened by low nutrient availability in soils, and this stress factor is greatly *amplified* by waterlogged and anoxic soils. Therefore, carnivory of most terrestrial carnivorous plants can be explained as an adaptation to *all* these stress factors. The extent of adaptation of carnivorous plant roots to waterlogging alone has not yet been studied. Nevertheless, as follows from first studies, roots rely on aeration diffusive mechanism in roots supported by exodermal diffusive barriers (Adamec, 2005; Adamec et al., 2006)

Terrestrial carnivorous plants have adapted to these unfavourable factors as typical stress-strategists by growing slowly (see below). They do not require a high supply rate of mineral nutrients from soils, as they are able to store nutrients in their organs and re-utilize them efficiently (Dixon et al., 1980; Adamec, 1997a, 2002). A weakly developed root system is a common characteristic of most carnivorous plants (Lüttge, 1983; Juniper et al., 1989, p. 21-22; Adamec, 1997a). The root:total biomass ratio ranges from only 3.4 to 23% in various carnivorous plants (Karlsson and Carlsson, 1984; Karlsson and Pate, 1992; Adamec et al., 1992; Adamec, 1997a, 2002). Roots are usually short, weakly branched, and able to tolerate anoxia and related phenomena ($H_2S$) in wet soils. They are able to regenerate easily. Generally, even in spite of an absence of any study on uptake of mineral ions by roots of carnivorous plants, it may be concluded for several reasons that the capacity of carnivorous plant roots for mineral nutrient uptake is limited, and compensated by nutrient uptake from prey. Yet, Adamec (2005) has recently studied the ecophysiological characteristics of carnivorous plant roots and has found that their aerobic respiration rate and water exudation rate per unit biomass is comparable with those reported in roots of non-carnivorous plants in the literature or even higher. Thus, roots of carnivorous plants are physiologically very active per unit biomass and well adapted to endure soil anoxia.

## 4. Animals as prey for plants: what an advantage?

Considering possible advantages of carnivorous plants to capture animals as prey, which could be substantial for the evolutionary ecology of carnivorous plants, at least two main aspects can be taken into account. One of the aspects can be ecological: as most carnivorous plant species are able to capture relatively small prey items (relative to plant or trap size, Karlsson et al., 1987; Givnish, 1989; Harms, 1999), which are abundant at sites (e.g. ants, small flies, mosquitoes, crustaceans, etc.), this fact ensures the relatively reliable catch of prey over a time, though there are very great differences in prey capture effectiveness (over 10 times) between individual plants even at the same microsite (Karlsson et al., 1987, 1994; Thum, 1989a,b). Moreover, many potential prey taxa are adapted to visiting plants for food. Thus, almost all carnivorous plants are able to capture at least some prey within a given time period.

The second aspect can be nutritional: as compared to plant tissue nutrient content (i.e. nutrient amount per unit dry biomass, DW) animals as prey represent a relatively rich source of some macrobiogenic mineral nutrients, and it is possible to consider that this relationship as the main benefit predetermined the evolution of plant carnivory from the very beginning. As stated above, typical wet, peaty or sandy soils inhabited by carnivorous plants have a very low available N, P, and K content but the tissue N and P content in prey carcasses is commonly about 5-10 times higher than that in carnivorous plant organs (see below), while the K content is comparable. Thus, it is possible to assume that it was N and P uptake from animal prey that represented the main benefit and evolutionary advantage of carnivorous plants to which these plants have adapted from the beginning of their evolution. The following total nutrient content was found in terrestrial insects or aquatic crustacean zooplankton ($g.kg^{-1}$ DW): N, 99-121; P, 6-14.7; K, 1.5-31.8; Ca, 1-44; Mg, 0.94 (Reichle et al., 1969; Watson et al., 1982; Wærvågen et al., 2002; DeMott et al., 2004; Woods et al., 2004). However, a part of insect nutrients is not available to carnivorous plants (Dixon et al., 1980; Adamec, 2002).

## 5. Mineral nutrition of carnivorous plants - general principles

The term mineral nutrition of plants includes processes of mineral nutrient uptake by plants from the ambient medium, nutrient translocation within the plant, incorporation of mineral nutrients to plant metabolism and physiological functions, release from primary physiological functions and of entry secondary ones. Our knowledge of mineral nutrition of carnivorous plants can still be considered to be fragmentary, as it is confined to about 50 species and less than 75 studies since the 1950's.

Although growing in mineral-poor habitats, both terrestrial and aquatic carnivorous plants have nearly the same composition of macroelements as non-carnivorous wetland and aquatic plants (Adamec, 1997a; Ellison, 2006; cf. Dykyjová, 1979). However, terrestrial carnivorous species have considerably lower foliar tissue content of macroelements than aquatic ones. Ellison (2006) has recently reviewed literature data on foliar nutrient content in terrestrial carnivorous plants to be on average 1.26% of DW for N (quartiles 0.9 and 1.9%), 0.094% of DW for P (quartiles 0.07 and 0.16%), and 0.75% of DW for K (quartiles 0.50 and 1.0%), and has compared them with those for non-carnivorous plants. As follows from his review mean tissue N, P, and K contents in terrestrial carnivorous plant leaves generally are lower than those in leaves of non-carnivorous, usually mesophytic plants (mean N 1.8% of DW, P 0.105%, K 1.9%) but great overlapping occurs, especially for N and P. After the foliar tissue N, P, and K content, out of all functional plant groups reviewed, terrestrial carnivorous plants resembled the groups of evergreen trees and shrubs most of all. In terrestrial carnivorous plant leaves, mean values could lie within 0.1-0.3% of DW for Ca and 0.2-0.3% for Mg (Adamec, 1997a, 2002). If compared, mean values in aquatic carnivorous plant leaves/shoots could lie within 1.5-2.5% of DW for N, 0.20-0.35% for P, 2.0-3.0% for K, 0.3-0.8% for Ca, and 0.2-0.4% for Mg (Adamec, 1997a, 2000, 2008b). However, three critical comments should be added to the issue of interpretation of tissue nutrient content in carnivorous plants. It is obvious that prey captured in traps of aquatic carnivorous plants were also included in the tissue nutrient contents (overestimated P and Ca content; see Adamec, 1997a). As leaf or shoot nutrient contents depend markedly on leaf/shoot age (senescence) or position on the carnivorous plant (Adamec, 1997a, 2000, 2002, 2008b) it must be always clear what was the age (or position) of the organ analysed. Furthermore, it has commonly been demonstrated in various carnivorous plant species that tissue nutrient content can remain unaffected or be even significantly lower after feeding on prey or soil fertilization, as a result of more rapid growth (Adamec, 1997a, 2000, 2002, 2008a). That is why tissue nutrient content alone is an unreliable measure of nutrient uptake by carnivorous plants, its interpretation value is limited, and plant growth rate should also be considered in relevant studies (Adamec, 2008a; Farnsworth and Ellison, 2008). Therefore, due to these objections, it is reasonable to determine also the nutrient stoichiometry of carnivorous plants to consider relative nutrient limitations of plant growth (Ellison, 2006). On the basis of this approach, the latter author could demonstrate a *co*-limitation of the growth of carnivorous plants in the field or natural soils by N + P or N + P + K, rather than *only* by N or P or K.

The most extensive process of mineral nutrition is photosynthetic fixation of $CO_2$ by leaves. All carnivorous plants are green and able to fix $CO_2$ (autotrophy) although the growth of some species (mainly aquatic) is partly dependent on organic carbon uptake from prey (facultative heterotrophy; see Lüttge, 1983; Adamec, 1997a). Many carnivorous plants of all taxonomic groups fix $CO_2$ according to the $C_3$ scheme of the Calvin cycle (Lüttge, 1983), but anatomical evidence in favour of the $C_4$ type has been given in 6 Mexican succulent *Pinguicula* species (Studnička, 1991). Generally, it is characteristic for photosynthesis that the maximum net photosynthetic rate per unit DW or leaf area ($P_{max}$) of leaves of terrestrial carnivorous plants is about 2-5 times (mean about 3 times) lower than that of other non-carnivorous plants (for the review see Ellison, 2006). Such a low photosynthetic rate presumably, reflects the relatively low growth rate of terrestrial carnivorous plants as typical S-strategists (see below). Generally low $P_{max}$ values in terrestrial carnivorous plants are further supported by their very low values of photosynthetic nutrient use efficiency for N and P. As reviewed by Ellison (2006) these mean values for carnivorous plants are about 3 times lower for N and about 2 times lower for P than those for terrestrial non-carnivorous plants. The relationship between carnivorous plants' photosynthetic performance and carnivory is, however, complex and ambiguous (Juniper et al., 1989). First, $P_{max}$ of traps is usually lower than that of other non-carnivorous leaves of the same plants, i.e. pitchers *vs.* phyllodia (Givnish et al., 1984; Ellison and Gotelli, 2002). Second, the photosynthetic effect of prey addition is quite different in different carnivorous plant species (cf. Mendéz and Karlsson, 1999; Ellison and Gotelli, 2002; Ellison and Farnsworth, 2005; Wakefield et al. 2005; Farnsworth and Ellison, 2008); the same characteristics hold also for aquatic carnivorous species (Adamec, 2008a). Nevertheless, at least in most *Sarracenia* species and in *Darlingtonia californica*, prey addition does significantly increase $P_{max}$ *sensu* the prediction by Givnish et al. (1984).

## 6. Mineral nutrition of carnivorous plants: mineral nutrient economy

The three principal processes of mineral nutrition determine the mineral nutrient budget in terrestrial carnivorous plants: foliar nutrient uptake from prey and root nutrient uptake from the soil, mineral nutrient reutilization from senescing shoots (mineral nutrient economy), and stimulation of root nutrient uptake by foliar nutrient uptake.

As follows from the detailed review by Adamec (1997a) based on numerous experimental data, uptake of the following mineral nutrients from prey carcasses or mineral nutrient solution by traps of various species of terrestrial (or partly also aquatic) carnivorous plants has been proven so far: N, P, K, Na, Ca, Mg, and S. Yet, the importance of a given macronutrient taken up from prey for a plant ecophysiological role depends on its uptake efficiency from prey carcasses. So far, only three studies have determined the nutrient uptake efficiency from model insect prey in terrestrial carnivorous plants and the greatest attention has been focused on N. In greenhouse-grown *Drosera erythrorhiza* fed on fruit flies (*Drosophila*), Dixon et al. (1980) found that 76% of the initial total N, having been contained in flies, had been taken up by the leaves. Obviously, a good deal of N in the spent flies was present in unavailable chitinous skeletons. However, much lesser efficiency (39-51 %) of N uptake from fruit flies was estimated in three north European *Pinguicula* species and *Drosera rotundifolia* in a greenhouse experiment (Hanslin and Karlsson, 1996); in field-grown plants, the efficiency was only 29-41%. Adamec (2002) compared the uptake efficiency from fruit flies and mosquitoes in greenhouse-grown *Drosera capillaris* and *D. capensis*. The uptake of N, P, K, and Mg was relatively efficient (43-62% N, 61-97% P, 60-96% K, 57-92% Mg), while that of Ca was not and depended greatly on tissue Ca content in the insects. Similar values of uptake efficiency from fruit flies (56-65% N, 59-67% P) follow indirectly from the greenhouse growth experiment in *D. closterostigma* (Karlsson and Pate, 1992). Thus, the uptake efficiency of P, K, and Mg from prey can be much greater than that of N but the true field-based values are still unknown. Contrary to certain knowledge of the efficiency of mineral nutrient uptake from prey by traps, there are still virtually *no* published data on the uptake affinity and capacity of roots of carnivorous plants for mineral ions, to be compared with those in non-carnivorous plants. It is possible to expect, however, that the root uptake affinity will be relatively high, while the uptake capacity (due to slow growth) will be very low.

A further typical ecophysiological characteristic of terrestrial carnivorous plants is their extraordinarily good mineral nutrient economy, such as very efficient reutilization (i.e. recycling) of N, P, and K from senescing leaves/shoots. Reutilization efficiency in various terrestrial carnivorous species was found to be 56-99% for N, 51-98% for P, and 41-99% for K (for details see Adamec, 1997a, 2002). Like in typical non-carnivorous plants, less efficient Mg reutilization and zero or even negative Ca reutilization were usually found in carnivorous plants. Mean reutilization efficiencies of N (70-75%) and P (75-80%) in carnivorous plant leaves or shoots are by 20-25 percentage points greater than those found in non-carnivorous bog or fen plants which usually grow at the same microsites (Adamec, 2002; cf. Aerts et al., 1999). This comparison shows that terrestrial carnivorous plants, in spite of their ability to take up needed nutrients from prey, make a great physiological effort to minimize mineral nutrient losses (of N, P, K) from senescing organs.

One of the typical and fascinating ecophysiological peculiarities of mineral nutrition in terrestrial carnivorous plants is a marked stimulation of root nutrition by foliar uptake of mineral nutrients from prey. The stimulation was repeatedly confirmed in about 10 terrestrial carnivorous species under greenhouse or field conditions within the last 25 years (e.g., Hanslin and Karlsson, 1996; Adamec, 1997a, 2002). Presumably, this represents one of the most important ecophysiological adaptations of carnivorous plants. Generally, in various growth experiments, carnivorous plants fed on insects or mineral nutrient solutions grew rapidly and accumulated much more mineral nutrients in their total produced biomass (about 1.6-27× more for N, P, K, Ca, and Mg as compared to unfed control plants) than they could take up theoretically from the limited foliar nutrient supply. Thus, stimulation of absorptive activity of roots is the essence of the very high efficiency of foliar nutrition for carnivorous plant growth. Only mineral, but not organic substances, caused this phenomenon. It means that mineral substances taken up by leaves from prey stimulated, in an unknown way, the activity of roots which then took up the amount of nutrients needed for increased growth from mineral-poor soil. It is possible to assume that the extent of this stimulation will be several times greater for K, Ca, and Mg uptake than that for N and P under natural conditions as prey are a rather poor source of these metallic cations. Hanslin and Karlsson (1996) proved in some carnivorous species in the field that the stimulatory effect on roots was of a quantitative nature, dependent on the amount of prey.

The essence of the stimulation of root uptake in carnivorous plants has not yet been explained. Adamec (2002) tried to explain this effect in three *Drosera* species. Slightly greater root lengths could only explain about 17% of the uptake stimulation, the higher theoretical uptake rate of roots per unit root biomass being only about 15-

30%, but the greater root biomass could explain to 70-85% of the effect. Metabolic root activity (as aerobic respiration), however, was unchanged. Moreover, the stimulatory effect on the roots was related to tissue mineral nutrient content in neither roots nor shoots. Although the total root biomass of the fed plants was markedly greater than that in unfed controls, the proportion of root biomass to the total biomass of fed plants mildly decreased, according to a theory. A crucial question is what mineral nutrients taken up by leaves from prey can stimulate root nutrient uptake in carnivorous plants? It could be phosphate alone (Karlsson and Carlsson, 1984) but the role of other nutrients (especially N) is as yet unknown.

## 7. Growth effects of carnivory

### 7.1. GREENHOUSE CONDITIONS

Many principal pieces of knowledge of mineral nutrition of terrestrial carnivorous plants have been obtained in greenhouse growth experiments (Adamec, 1997a). As these experiments represent a considerable simplification of true natural conditions (e.g. lack of competition, mortality, and rain), results reflect the *potential* physiological abilities of carnivorous plants to take up mineral nutrients by leaves from prey or roots from soil, rather than the ecological importance of carnivory. It has been found in all terrestrial carnivorous species studied that they can grow satisfactorily in natural peaty soils even without additional feeding on prey or soil fertilization. However, foliar fertilization by droplets of a mineral nutrient solution (Karlsson and Carlsson, 1984; Adamec et al., 1992; Adamec, 2002) had about the same positive growth effect as model feeding on prey and proved that the absorbed mineral nutrients from prey, especially N and P, but not organic substances, were of principal importance for plant growth. Overall, depending on experimental conditions, feeding on prey or soil fertilization could increase the growth rate and mineral nutrient uptake of carnivorous plants as much as several times (for the review of experiments see Adamec, 1997a and Ellison, 2006). However, on the basis of many greenhouse-growth experiments, it has been concluded that terrestrial carnivorous plant species differ greatly in their ability to use soil or foliar mineral nutrient supply for their growth and, accordingly, carnivorous plants have been classed into three main ecophysiological groups (Adamec, 1997a). Plants in the largest group of ‘nutrient requiring species’ increase markedly their growth due to both soil and leaf nutrient supply and their root nutrient uptake may be stimulated by foliar uptake. These species grow relatively rapidly in rather wet habitats, sometimes with mildly increased soil nutrient content. Plants in the group of ‘root-leaf nutrient competitors’ grow better and accumulate more nutrients thanks to both root and leaf nutrient uptake. However, competition occurs between root and leaf nutrient uptake. This group includes especially some Australian *Drosera* species from drier areas. Plants in the third group of ‘nutrient modest species’ have roots with a very low nutrient uptake capacity and rely on leaf nutrient uptake. This group includes some Australian pygmy sundews and also *Dionaea muscipula*.

### 7.2. NATURAL CONDITIONS

Field studies show clearly the ecological importance of carnivory for carnivorous plant growth and development under the conditions given. They include both competition and mortality, but also robbing of prey by opportunistic predators (kleptobionts, kleptoparasites) and washing out of nutrients from prey or washing away whole prey by heavy rains (Adamec, 1997a). In analogy with greenhouse experiments, natural capture of prey or feeding on extra prey in various terrestrial carnivorous plants under natural (or outdoor) conditions resulted in replicate growth increase which was comparable with that stated for greenhouse experiments (for the review see Adamec, 1997a and Ellison, 2006). Moreover, the real ecological importance of carnivory in individual cases always depended on the amount on captured prey in which even closely placed individuals of the same species within the same micropopulation differed 10 times or more (Karlsson et al., 1987, 1994; Thum, 1989a,b). Thus, the amount of captured prey has proven to be the principal ecological factor for the natural growth and vigor of carnivorous plants. The differences in prey capture between the individiuals might lead to size differentiation within the plant population (Thum, 1988). In this line, experiments on supplementary feeding of 5 European carnivorous plant species on prey proved that the plants were able to use much more prey for their enhanced growth or nutrient accumulation than they really could capture naturally (Thum, 1988; Chapin and Pastor, 1995; Hanslin and Karlsson, 1996). Therefore, the ecophysiological capacity to digest and utilize nutrients from prey is very high but usually not fully used under natural conditions.

The classic cost-benefit model of plant carnivory by Givnish et al. (1984) predicts that carnivory will be beneficial only in nutrient-poor soils. To test this model, Ellison (2006) pooled available data on 29 studies on growth experiments of carnivorous plants (influence of prey and soil fertilization), both under greenhouse and field conditions. A meta-analysis of these data showed clearly a significant positive growth effect of prey capture or addition ($p=0.02$) but no significant effect of soil fertilization ($p=0.15$) or nutrient × prey interaction ($p=0.81$). It means that the effect of mineral fertilization of natural peaty soils may not lead to growth increase in carnivorous plants, though it was proven in some studies (e.g. Svensson, 1995), and that an efficient use of prey is not confined to nutrient-poor soils (*sensu* Karlsson et al., 1991). As the level of soil fertilization was very different in single studies (see Adamec, 1997a) and could also be supraoptimal, it is hardly possible to generalize these experiments.

Prey capture is much more important for seedlings and small plants than for adult ones. Due to their small size, prey capture by seedlings is considerably limited but it leads, in successful individuals, to much faster growth and attaining maturity, and, therefore, to prolific flowering and seed set (Thum, 1988). Faster trap growth then allows more efficient capture of larger prey (i.e., positive feedback). Probably, capture of prey in adult plants supports flowering and seed set to the same extent as vegetative growth but it markedly speeds up reaching the minimum plant size necessary for flowering. As a result of capturing prey, terrestrial carnivorous plants also markedly strengthen their competitive abilities (Wilson, 1985).

Under natural conditions, the ecological importance of carnivory concerning mineral nutrition mainly depends on what proportion of needed mineral nutrients (as seasonal nutrient gain or consumption) carnivorous plants take up directly from prey during their seasonal growth (Adamec, 1997a). Coming from measured rates of seasonal prey capture and usually a 76% efficiency of nutrient uptake from prey (after Dixon et al., 1980), the calculated values of the proportion listed in Table 1 are rather variable among different plant species but also within a species, as dependent on differential seasonal prey capture. Overall, carnivorous plants at various sites can compensate by carnivory as much as 7-100% of their seasonal gain of N and the same amount of P, but only a small proportion of K (1-16%) and perhaps less Ca and Mg. These data indicate that the main ecological consequence of carnivory is to obtain the greatest proportion of seasonal N and P gain from prey as possible since N and P are often the most (co-)limiting nutrients in peaty soils. Nevertheless, as shown by Hanslin and Karlsson (1996) for three *Pinguicula* species the mean *direct* N uptake from extra added prey amounted to only 39% of the total increased N amount, while the rest (i.e. 61% N) was taken up *indirectly* from the soil, as a result of the root uptake stimulation (see 6). Due to low proportion of K, Ca, and Mg uptake from prey, the stimulated uptake of these elements from soil by roots should be the greater. Generally, it is possible to conclude that carnivory is ecologically very important for most species under natural conditions.

TABLE 1. Mean or range of seasonal mineral nutrient gain coming from carnivory (in %) in terrestrial carnivorous plant species under natural conditions after different authors

| Species | N | P | K | Reference |
|---|---|---|---|---|
| *Pinguicula vulgaris* | 26-40 | 36 | 7-16 | Karlsson (1988); Karlsson et al. (1994) |
| *Pinguicula alpina* | 8-14 | 12-19 | 1.3-1.9 | -“- |
| *Pinguicula villosa* | 7-15 | 6-10 | 3-12 | -“- |
| *Drosera rotundifolia* | 63 | 95 | 1.1 | Thum (1988) |
| *Drosera intermedia* | 92 | 100 | 1.6 | Thum (1988) |
| *Drosera erythrorhiza* | 11-17 | -- | -- | Dixon et al. (1980) |
| -“- | 100 | 100 | 2-3 | Watson et al. (1982) |

## 8. Ecophysiology of aquatic carnivorous plants

### 8.1. INTRODUCTION

About 50 species belonging to the genera *Aldrovanda* (waterwheel plant, Droseraceae) and *Utricularia* (bladderwort, Lentibulariaceae) are submerged aquatic or amphibious carnivorous plants (Juniper et al., 1989; Taylor, 1989; Guisande et al., 2007). Unlike the dominant majority of aquatic non-carnivorous plants, all aquatic carnivorous species are strictly rootless and, therefore, they can take up mineral nutrients for their growth from the ambient medium and from captured prey *only* via their shoots. Nevertheless, they fulfill all three principal functional criteria generally placed on carnivorous plants (see above). Traps of aquatic species exhibit rapid movements, which are among the most rapid within the plant kingdom, and represent fascinating objects for a biological study

(Juniper et al., 1989). However, the main focus of ecophysiologists has always been the study of processes in terrestrial, rather than aquatic, carnivorous species (cf. Juniper et al., 1989; Adamec, 1997a). Moreover, mainly due to methodological problems, the ecophysiological study of the latter group has lagged much behind that of the former group. As both ecological groups of carnivorous plants are rather dissimilar in their principal morphological and physiological features and also *per se* (submerged *vs.* terrestrial life *sensu* Colman & Pedersen, 2008), it is reasonable and justifiable to distinguish between these groups when making ecologically or physiologically oriented reviews.

## 8.2. ECOLOGICAL CHARACTERISTICS OF HABITATS OF AQUATIC CARNIVOROUS PLANTS

Aquatic carnivorous plants usually grow in shallow standing or slowly streaming humic (i.e. dystrophic) waters, often together with vascular aquatic non-carnivorous plants. It may be assumed that the former plant group also tolerates very high concentrations of humic acids and tannins (very dark waters), while the latter plant group usually does not. At these sites, the sum of the concentration of humic acids and tannins is commonly within the range 5-20 $mg.l^{-1}$ and may even extend to 60 $mg.l^{-1}$ (Adamec, 2007a, 2008b). The waters are usually poor in mineral N ($NH_4^+$, $NO_3^-$) and P (the concentration of both commonly 5-20 $\mu g.l^{-1}$), but also in K (<0.5 $mg.l^{-1}$). If the site is not impacted by human activity, the concentrations may be 5-10 times lower (see Adamec, 1997a; Guisande et al., 2007). The concentrations of $SO_4^{2-}$, Ca, Mg, and Fe, however, are usually >1 $mg.l^{-1}$ (Guisande et al., 2007) and do not limit plant growth. A partly decomposed, nutrient-poor litter of reeds and sedges usually accumulates in these waters. The slowly decomposable litter gradually releases mineral nutrients, humic acids, tannins, and $CO_2$. Hence, the waters are usually rather high in free [$CO_2$] (0.1-1 mM; Adamec, 1997a,b, 2007a, 2008b, c). A high [$CO_2$] >0.15 mM was found to be the principal water chemistry factor supporting vigorous growth and propagation of stenotopic *Aldrovanda vesiculosa* (Adamec, 1999). The same relationship between [$CO_2$] and growth holds true also in aquatic non-carnivorous plants. In addition, reduced concentrations of dissolved oxygen, within the range 0.0-12 $mg.l^{-1}$, were found at many sites of aquatic carnivorous plants (Adamec, 1997b, 1999, 2007a; Guisande et al., 2000, 2004; Adamec and Kovářová, 2006; Giural and Rougier, 2007). Moreover, the latter authors found a marked daily oscillation of [$O_2$]. The majority of aquatic carnivorous species usually grow in soft to moderately hard (total alkalinity 0.2-2 $meq.l^{-1}$), acid or neutral waters (pH 5-7.5), but some temperate-zone species may also grow in hard and alkaline waters (pH 8-9.3; see Adamec, 1997a). Two wide-spread aquatic species, *Utricularia australis* and *U. minor*, were able to grow in a very wide range of pH, the former species within 4.3-8.3, the latter within 3.5-9.3 (cf. Adamec, 1997a, 2008b; Navrátilová and Navrátil, 2005). Thus, in eurytopic species at least, water pH alone is not important for their field growth.

Whilst considering photosynthetic cost-benefit relationships, Givnish et al. (1984) postulated that, for terrestrial carnivorous plants, carnivory is only beneficial in nutrient-poor, moist, and sunny habitats. However, many aquatic carnivorous species in their typical habitats do not comply, as irradiance is often very low (<5% of that in the open; Adamec, 2008b) though comparable with that for other aquatic non-carnivorous species.

## 8.3. GROWTH CHARACTERISTICS OF AQUATIC CARNIVOROUS PLANTS

Aquatic carnivorous plants markedly differ morphologically and ecophysiologically from terrestrial species: they are always rootless, floating freely below the water surface, or are weakly attached to loose sediments, submerged or partly amphibious (Taylor, 1989; Guisande et al., 2007). Most species have a linear and modular shoot structure consisting of regularly changing nodes with filamentous leaves and tubular, fragile internodes. In some species, the leaves are arranged in true whorls. Only several species (e.g. *Utricularia volubilis*) are rosette-shaped plants. The majority of linear-shoot species have homogeneous (monomorphic), non-differentiated green shoots bearing traps (e.g. *Aldrovanda vesiculosa, Utricularia vulgaris, U. australis, U. inflata*). Several species (e.g. *Utricularia intermedia, U. floridana*) have dimorphic shoots differentiated into green photosynthetic ones (usually bearing only a few or no traps) and pale carnivorous (trapping) ones with many traps. These species are intermediate in body plan between the aquatic *Utricularia* species with monomorphic shoots and terrestrial species (e.g. *U. uliginosa, U. livida*) with aboveground, flat green leaves and belowground, pale carnivorous shoots bearing traps (Taylor, 1989).

Aquatic carnivorous plants exhibit some growth characteristics differentiating them distinctly from all terrestrial carnivorous species (Adamec, 1997a). Firstly, adult plants maintain the length of the main shoot approximately constant throughout the season: they show very rapid apical shoot growth but their basal shoot segments age and die at about the same rate (“conveyer-belt“ shoot growth system). Thus, the new biomass is allocated into branching or flowering only. Under favourable conditions, the apical shoot growth rate of aquatic species with linear shoots was 1.0-1.2 whorls.d$^{-1}$ in *Aldrovanda* (Adamec, 2000; Adamec and Kovářová, 2006) and even greater in field-grown *U. vulgaris* (1.4-2.8 nodes.d$^{-1}$, Friday, 1989) or *U. australis* (2.8-3.5 nodes.d$^{-1}$, Adamec and Kovářová, 2006). Suprisingly, the apical growth rate of *U. australis* was 2.9-4.2 nodes.d$^{-1}$ also in an oligotrophic water, though the relative growth rate (RGR) was zero (Adamec, 2008c). Thus, very high apical growth rate in aquatic species may not be connected with high RGR. It is also an important strategy in competition with epiphytic algae, which usually densely cover their older shoots (Friday, 1989). In the slowly growing subtropical *U. purpurea*, however, the apical growth rate was only 0.25 nodes.d$^{-1}$ (Richards, 2001). Unlike all terrestrial carnivorous plants, representing typical S-strategy, high RGRs were reported for a few aquatic species under favourable conditions which rather suggests their R-strategy. The doubling time of biomass (i.e., $\log_e 2$ /RGR) in field-grown *Aldrovanda* was only 8.4-21.5 d (Adamec and Kovářová, 2006) or 12.9-23.0 d (Adamec, 1999) and 12.8 d in an outdoor culture (Adamec, 2000), 9.1-33.2 d in field-grown *U. australis* (Adamec and Kovářová, 2006), or 12.4-23.1 d in greenhouse-grown *U. vulgaris, U. geminiscapa, and U. purpurea* (Pagano and Titus, 2004, 2007). Pagano and Titus (2007) proved about a two- to threefold RGR increase in the three *Utricularia* species as a result of [$CO_2$] increase. Comparable values between 6.4-34.7 d were recorded by Nielsen and Sand-Jensen (1991) for aboveground biomass in 12 rooted submerged, non-carnivorous species. In contrast, the corresponding values for terrestrial species of the genera *Drosera*, *Genlisea*, and *Sarracenia* are much greater (21-104 d, mean about 35-40 d), suggesting their considerably slower growth (Adamec, 2002, 2008d; Farnsworth and Ellison, 2008).

The very rapid growth of rootless aquatic carnivorous plants in nutrient-poor habitats requires ecophysiological adaptations that enable the plants to access the highly limited supplies of mineral nutrients from the water. These adaptations include carnivory, efficient nutrient re-utilization from senescing shoots, and a very efficient nutrient uptake from water (Kamiński, 1987; Kosiba, 1992; Friday and Quarmby, 1994; Adamec, 2000, 2008a, b; Englund and Harms, 2003).

Another important growth characteristic, which facilitates propagation, is the production of shoot branches which subsequently develop into separate, new individuals (Adamec, 1999). The branches of *Aldrovanda* always develop into new plants, but in some aquatic *Utricularia* species, once initiated, branches may not develop beyond the early stages (Adamec, 2008c). It is generally accepted that the number of branches per shoot is the principal growth parameter to be used as a criterion for plant vigor and propagation rate and therefore also reflects the suitability of a habitat for plant growth (Kamiński, 1987; Adamec, 1999, 2000, 2008c, Adamec and Kovářová, 2006). In some aquatic carnivorous species studied, branching rate (number of internodes between two branches) was regular under optimum conditions and species specific (*Aldrovanda*: mean 6.2, range 3-11, Adamec, 1999; *U. stygia*: 12.2±0.4 in photosynthetic shoots, 6.7±0.2 in carnivorous shoots; *U. intermedia*: 16.8±0.4 in photosynthetic shoots, 5.9±0.1 in carnivorous shoots, Adamec, 2007a; *U. australis*: 22.1±1.2 or 10.5±0.4, Adamec, 2008c). The latter data indicate that, although branching rate is genetically fixed, it is under ecological regulation. If branching rate is divided by the apical shoot growth rate, this parameter - the branching frequency - characterises the real time involved in initiating successive branches on the shoot. Thus, branching frequency is a good criterion for RGR (Adamec and Kovářová, 2006). The authors found a similar branching frequency (4.7-5.5 d.branch$^{-1}$) for field-grown *Aldrovanda* and *U. australis.* In both species, however, competitive processes occurred between the production of new whorls and branches. Evidently, knowledge of branching traits is crucial for understanding growth characteristics in aquatic *Utricularia* species.

## 8.4. TRAP ECOPHYSIOLOGY OF AQUATIC *UTRICULARIA* – MYSTERIES ASSOCIATED WITH PREY DIGESTION. HOW IMPORTANT ARE COMMENSALS?

*Utricularia* suction traps are hermetically closed bladders functioning on the basis of underpressure (e.g. Sydenham and Findlay, 1975; Juniper et al., 1989; Guisande et al., 2007). The trap size in aquatic species is within the range 1-6 mm, rarely up to 12 mm (Taylor, 1989); these are larger than the traps of terrestrial species in the genus. Though they are the smallest of all carnivorous plants, they are considered the most sophisticated traps functionally (Juniper et al., 1989). Contrary to the traps of other species, solutes and suspended particles sucked-in from the ambient water are retained hermetically in the lumen until the trap is senescent. Four types of glands (hairs) occur inside or outside the traps; abundant and large internal quadrifid and bifid glands are principal for trap physiology (see Juniper et al., 1989; Guisande et al., 2007).

Commensal microorganisms (mainly bacteria, algae (*Euglena*), ciliates, rotifers; e.g., Richards, 2001) occur and propagate in the traps of many aquatic *Utricularia* species. The question of their role in trap functioning and possible benefit for plants is often discussed. Presumably, some of these commensals participate, to various extent in prey digestion by producing their own enzymes (Richards, 2001; Sirová et al., 2003), which has been demonstrated for phosphatases in commensal bacteria and unicellular algae (Płachno et al., 2006; Sirová et al., unpubl.). A slightly reduced growth of the wetland species *U. uliginosa* after the feeding on *Euglena* culture as prey (Jobson et al., 2000) suggests that the real relationship may even be slightly parasitic. Nevertheless, for some aquatic *Utricularia* species with low trapping efficiency (e.g., *U. purpurea*) in barren waters, commensal communities in traps seem to be more beneficial for the plants than the trapping of prey alone (Richards, 2001; Sirová et al., unpubl.). As shown very recently, commensals presumably participate in providing the traps without prey with N and P (Sirová et al., unpubl.). In traps without prey, which had sucked in some detritus or phytoplankton from the ambient water during incidental firings, a miniature microbial food web may run. Its main components are bacteria, Dinophyta, ciliates, and rotifers. Similar interactions were found in the digestion fluid in *Sarracenia* pitchers (Gray et al., 2006). Moreover, in filtered fluids from empty traps of two field-grown *Utricularia* species, high concentrations of organic carbon (60-310 $mg.l^{-1}$), both glucose and fructose (8-24 $mg.l^{-1}$), organic N (7-25 $mg.l^{-1}$), and soluble P (0.2-0.6 $mg.l^{-1}$) were detected (Sirová et al., unpubl.). The concentrations usually increased with trap age and correlated with commensal biomass. Traps presumably support the run of this microbial food web energetically by supplying organic matter, which is in relative excess for the plant, and as a trade-off for this, they obtain growth limiting N and P from decomposed detritus or phytoplankton. Thus, aquatic *Utricularia* species, which grow in very oligotrophic habitats with low prey availability, are rather “bacterivorous” or “detritivorous” than carnivorous. The $N_2$ fixation mediated mainly by cyanobacteria occurred on the outer trap surface in *U. inflexa* (Wagner and Mshigeni, 1986). Owing to the specific chemical conditions, it could also run inside the traps and provide the traps with N.

Surprisingly, zero $O_2$ concentration was consistently detected in the fluid of excised and intact traps (without prey) of six aquatic *Utricularia* species bathed in an oxygenated medium, regardless of trap age and irradiance (Adamec, 2007b). Thus, there is normally anoxia inside the traps which can incidentally be interrupted due to trap firing (trapping of prey or another irritation) for short periods of time. The potential aerobic respiration of the inner glands and trap walls is so high that all $O_2$ is exhausted to zero within 10-40 min. The traps can pump out water and reset the underpressure within 30 min, which requires high amounts of energy derived from aerobic respiration and is prevented by respiration inhibitors (Sydenham and Findlay, 1975). Yet, it is not clear how the traps (glands) provide sufficient ATP energy for their demanding functions under anoxia, though a mitochondrial mutation of cytochrome *c* oxidase found in *Utricularia* should provide greater energetic power for the traps (Laakkonen et al., 2006). In traps with captured prey, anoxia causes prey to die of suffocation, while all trap commensals are adapted to facultative anoxia (Adamec, 2007b).

A pH value of 5.0±0.1 occurred in trap fluid in four aquatic *Utricularia* species independently of digestion of prey (Sirová et al., 2003). This suggests that trap fluid pH is well regulated. Though several types of hydrolytic enzymes were described from *Utricularia* traps using biochemical and cytochemical methods (protease, esterase, acid phosphatase; see Juniper et al., 1989), only the activity of phosphatases at pH 4.7 was determined as significant by an *in-situ* analysis of empty trap fluid in four aquatic *Utricularia* species (Sirová et al., 2003). Trap activities of α- and β-glucosidases, β-hexosaminidases, and aminopeptidases at the pH of 4.7 were usually lower by one or two orders of magnitude and were usually higher in the culture water at the same pH. Thus, a large proportion of the trap enzymatic activity, with the exception of phosphatases, entered the traps from the ambient water after firing. Generally, the activity of all enzymes was independent of prey digestion and was not inducible by prey. The absence of aminopeptidases (proteases) in traps could be compensated by the autolysis of prey tissues. Consistently high trap activities of phosphatases in all species imply that P uptake from prey or detritus might be more important than that of N for the plant.

## 8.5. PHOTOSYNTHESIS OF AQUATIC CARNIVOROUS PLANTS

While the (maximum) net photosynthetic rate ($P_{max}$) per unit DW or area of leaves of slowly growing terrestrial carnivorous species is, on average, 2-5 times lower than that in different functional groups of terrestrial non-carnivorous species (Ellison, 2006; see 5), $P_{max}$ in aquatic species (seven species, 40-120 mmol $O_2$ $kg^{-1}$ fresh weight.$h^{-1}$) is comparable with the highest values found in aquatic non-carnivorous species (30-110 mmol $kg^{-1}$ fresh weight.$h^{-1}$, Adamec, 1997b, 2006). Thus, very high $P_{max}$ is typical for aquatic carnivorous species with rapid growth but is also a prerequisite for this rapid growth as the rapid, permanent decay of senescent shoot segments causes a great loss of structural and non-structural carbohydrates (Adamec, 2000). In amphibious carnivorous species with dimorphic shoots, $P_{max}$ of photosynthetic shoots can increase considerably if the shoots become emergent (Colmer and Pedersen, 2008).

Traps of aquatic species as physiologically very active organs have high respiration rates (RD) and represent great photosynthetic costs, as hypothesized by Givnish et al. (1984). In six aquatic *Utricularia* species, trap RD per unit fresh weight (5.1-8.6 mmol.$kg^{-1}$.$h^{-1}$) was 1.7-3.0 times greater than that in leaves on carnivorous or photosynthetic shoots and nearly-maximum $P_{max}$ in photosynthetic leaves exceeded that in the traps (5.2-14.7 mmol.$kg^{-1}$.$h^{-1}$) 7-10 times (Adamec, 2006). Thus, very high RD:$P_{max}$ ratio in traps of these species (50-140%), unlike that in leaves (3.6-8.2%), means that there are high maintenance and photosynthetic costs of traps: in *U. stygia* and *U. intermedia* with dimorphic shoots, the trap RD could amount to 34-44% of the total plant respiration, while 63% in *U. australis* with monomorphic shoots (Adamec, 2006, 2007a, 2008b). However, in *U. macrorhiza*, mean trap RD was only about 10% higher than that in leaves and trap $P_{max}$ in lake water was as much as 41-67% of that in the leaves (Knight, 1992); similarly 67% in *Aldrovanda* (Adamec, 1997b).

Aquatic carnivorous plants usually grow in waters with high $[CO_2]$>0.1 mM. This fact is very important as all aquatic species tested so far use only $CO_2$ for photosynthesis (see Adamec, 1997a, b; Adamec and Kovářová, 2006; Pagano and Titus, 2007). The recent finding of slight $HCO_3^-$ use in *U. australis* induced by growing at high pH of about 9.2 (Adamec, 2008c) deserves further study. Generally, in several aquatic carnivorous species growing in the field or culture, $CO_2$ compensation points ($CO_2$ CPs) fell within the range 1.5-13.2 μM (Adamec, 1997a, b, 2008c; Adamec and Kovářová, 2006; Pagano and Titus, 2007); similar values of 1.5-10 μM are reported in aquatic non-carnivorous plants (Maberly and Spence, 1983). In 17 culture-grown species or accessions of aquatic carnivorous plants of both genera, $CO_2$ CPs (mean 5.3 μM, range 1.9-13.6 μM) were similar to those found in these species growing *in vitro* (mean 5.2 μM, range 2.5-8.8 μM; Adamec, unpubl.). A highly significant relationship was found between the $CO_2$ CP values and [$CO_2$] in the culture water. Similarly, $CO_2$ CPs in *U. australis* growing at 17 sites of different trophic levels ranged within 0.7-6.1 μM (mean 2.6 μM) but correlated significantly with neither of the internal or water chemistry factors nor with the capture of prey (Adamec, 2008c).

The influence prey capture on $P_{max}$ and RD was investigated in *Aldrovanda* and *U. australis* growing in an outdoor culture (Adamec, 2008a). Though both species fed on zooplankton grew significantly faster than unfed ones, feeding increased $P_{max}$ by 59% in *Aldrovanda* but decreased it by 25% in *U. australis.* $CO_2$ CP was unchanged due to feeding in *Aldrovanda* but increased from 5.2 to 9.2 μM in *U. australis.* The RD values stayed unchanged in both species. Thus, the hypothesis by Givnish *et al.* (1984) on stimulation of photosynthesis by catching prey has not been supported, although more data are needed. Carnivory should partly compensate for photosynthetic $CO_2$ uptake, but the uptake of organic carbon from prey in aquatic carnivorous plants has never been quantified. Yet, organic carbon uptake from prey in aquatic species may be ecologically important under $CO_2$ shortage (see Adamec, 1997a): field-grown *Aldrovanda* was also able to grow at pH>9.0 when catching numerous prey (Adamec, 1999), and greenhouse-grown *U. vulgaris* fed on prey grew better and branched more only at higher pH values of 7.6-9.1 (Kosiba, 1992).

## 8.6. MINERAL NUTRITION IN AQUATIC CARNIVOROUS PLANTS

Although rootless aquatic carnivorous plants grow in mineral-poor habitats they have similar macroelement composition to rooted aquatic non-carnivorous species (cf. Dykyjová, 1979; Adamec, 1997a; 2008a, b). Their tissue nutrient content (% DW) in young shoots is usually between 1.0-4.0 for N; 0.12-0.50 P; 1.5-5.0 K; 0.15-3.0 Ca; 0.2-0.7 for Mg. *U. australis* growing in very oligotrophic waters with low prey availability kept a relatively high shoot nutrient content (Adamec, 2008b). Regardless of a marked polarity of tissue N, P, and Ca content along shoots and the great differences between leaves and traps (Adamec, 2000, 2008b), mean shoot content of these five macroelements in aquatic carnivorous plants is about 1.5-3 times greater than that in terrestrial carnivorous plant leaves (cf. Ellison, 2006; see 5) and could reflect much faster growth in aquatic species. A marked polarity of tissue N, P, Ca content, indicating a very efficient N and P reutilization from senescing shoot segments, was found in rapidly growing aquatic species (Adamec, 1997a, 2000, 2008b). The Ca polarity was opposite, whereas K and Mg contents were constant. Culture-grown *Aldrovanda* reutilized 88% N and 67% P (Adamec, 2000) and field-grown *U. australis* on average only 48% N and 72% P (Adamec, 2008b). However, the slowly growing *U. purpurea* re-utilized only 37% N and 71% P (see Adamec, 1997a). Moreover, a very effective reutilization of N and P can be assumed in autumnal shoots forming turions (Adamec, 2000). Thus, aquatic species permanently lose only a relatively small part of their N and P in their senescent shoots (like terrestrial species; Adamec, 1997a) but all K, Ca, and Mg. Zero K reutilization in senescent shoots of aquatic species greatly contrasts with very efficient K reutilization in terrestrial ones (41-99%, see 5; Adamec, 2002).

Considerable differences in tissue nutrient content occur between shoots and traps in aquatic carnivorous plants of both genera. The content of N, Ca, and Mg is usually greater in photosynthetic shoots than in the traps, while the opposite is true for P and K demonstrating a considerable “mineral“ cost of carnivory (Adamec, 2008b; unpubl.). In *U. australis* with monomorphic shoots and mean proportion of trap DW 38%, traps in adult shoots contained about 30% total N, 53% P, and 51% K within the shoots (Adamec, 2008b).

Aquatic carnivorous species grow in oligo-mesotrophic waters in which [$NH_4^+$] usually strongly dominates over [$NO_3^-$]. *Aldrovanda* and some aquatic *Utricularia* species preferentially took up $NH_4^+$ to $NO_3^-$ from diluted $NH_4NO_3$ solutions (Adamec, 1997a, 2000; Fertig, 2001). Phosphate uptake by *Aldrovanda* apical shoot parts was two times faster than that by basal parts, but the finding that *Aldrovanda* takes up $K^+$ only via the basal parts (Adamec, 2000) still requires a deeper explanation. Besides, aquatic species can take up a substantial amount of mineral nutrients also from prey. Yet, only Friday and Quarmby (1994) have quantified an efficiency of N uptake from prey in aquatic species. In *U. vulgaris* fed on mosquito larvae, they estimated the efficiency of N uptake to be at least 83% of the total prey N. About 52% total plant N was obtained from the prey. Probably, the efficiency of N uptake from prey in *Utricularia* traps may be even higher than that in terrestrial species (cf. Adamec, 2002, see 6). P was also taken up rapidly from the prey but P reutilization from old shoot segments was much better than that of N.

There are several data showing marked effects of prey utilization on the growth of aquatic species, both in a culture and in the field (for the review see Adamec, 1997a; 2000, 2008a; Englund and Harms, 2003). Feeding led to longer shoots, greater DW, faster apical shoot growth, greater RGR, and, especially, increased branching as a main means of propagation. Thus, carnivory in aquatic species is at least as important as in terrestrial ones. However, it is still unclear how this growth effect of carnivory is induced since tissue N and P contents in apical or young shoot segments in prey-fed plants were lower compared to unfed plants (Adamec, 2000, 2008a).

Another important ecological parameter associated with mineral nutrition is the proportion of seasonal (daily) N and P gain obtained from prey. In *U. macrorhiza,* the proportion of seasonal N gain from carnivory was estimated to be about 75% (Knight, 1988). In robust *U. foliosa* growing at a nutrient-poor site with extremely low prey availability in Florida, the mean proportion was only about 0.9% N and 3.5% P (Bern, 1997). At sites with greater prey availability, these values could be one order of magnitude higher. Using a model containing literature-based data (Adamec, 1997a, 2000, 2008b; Adamec and Kovářová, 2006), it is possible to calculate which proportion of the daily N and P gain can be obtained due to capturing one small *Cyclops* (DW 25 μg) daily in *Aldrovanda* and *U. australis*. In rapidly growing plants (plant biomass doubled in 15 d) this covers about 15% daily N and 4% P gain in smaller *Aldrovanda*, while only about 0.62% N and 0.56% P gain in larger *U. australis*. However, if plant growth is zero and the plants maintain constant biomass, which is the case under unfavourable growth conditions, then it covers up to 100% daily N and about 16% P gain in *Aldrovanda* and about 1.8% N and 2.6% P gain in *U. australis.* Like in terrestrial species, the estimated values show that the ecological importance of N and P uptake from prey depends primarily on the quantity of captured prey. Capture of prey in aquatic species is thus one of the decisive factors for their rapid growth and especially for their propagation.

### 8.7. REGULATION OF INVESTMENT IN CARNIVORY IN *UTRICULARIA*

In aquatic *Utricularia* species, the proportion of traps to the total plant biomass as the structural cost (investment) in carnivory is 10-65%, but this proportion is regulated flexibly by the plants to minimize the costs of carnivory according to habitat factors: particularly water chemistry, prey capture, and irradiance (Knight and Frost, 1991; Friday, 1992; Bern, 1997; Guisande et al., 2000, 2004; Richards, 2001; Englund and Harms, 2003; Manjarrés-Hernández et al., 2006; Porembski et al., 2006; Kibriya and Jones, 2007; Adamec, 2007a, 2008b). Moreover, this regulation may be different in various species. Yet, in most cases, increased mineral nutrient availability either in the ambient water or prey led to decreased investment in carnivory in the terms of trap number per leaf or proportion of trap biomass. The number of traps per leaf in *U. foliosa* decreased in waters with increasing [$NO_3^-$] but simultaneously decreasing prey capture (Guisande et al., 2004). Thus, it is not possible to separate both factors. However, the number of traps per leaf in the same species correlated statistically significantly (inversely proportionally) with shoot P and especially N content (Bern, 1997). Out of all nutrient factors investigated in field-grown *U. australis*, only tissue N content in young shoot segments significantly (negatively) correlated with trap proportion (Adamec, 2008b). These results consistently support the "nutrient" hypothesis that all external nutrient factors, which decrease tissue N content in young shoots (poor prey capture, low [$NH_4^+$], high [$CO_2$], etc.), increase trap production in young shoots and *vice versa*, as a negative feedback regulation. This finding is consistent with the suggestion of Guisande et al. (2004) that ambient N sources are a limiting factor regulating investment in carnivory. However, Kibriya and Jones (2007), studying *U. vulgaris*, proposed a central regulatory role for P. This negative feedback also helps to stabilize the tissue contents of other mineral nutrients. As prey capture also supports plant growth, growth rate itself is obviously a component of this endogenous regulatory system. Moreover, some data show that the "nutrient" regulation of trap proportion in aquatic *Utricularia* is subject to photosynthetic regulation (Bern, 1997; Englund and Harms, 2003; Adamec, 2008b). At low photosynthetic rate (low irradiance, [$CO_2$]), trap proportion is relatively low or even zero.

## 9. Is plant carnivory beneficial: when and why? Nutritional cost-benefit relationships of carnivory

In their natural habitats, carnivorous plants grow *together* with non-carnivorous species (e.g. bog and fen species of graminoids, cyperoids, and Ericaceae) and it is evident that both plant groups are subjected to exactly the same ecological conditions; the same conclusion may also hold true for aquatic carnivorous plants. Carnivory is thus only one of many possible adaptation strategies to combined unfavorable conditions occurring in nutrient-poor and wet soils. Yet, when and why can this ecological adaptation be beneficial? Based on studying carnivorous bromeliads, Givnish et al. (1984) predicted in their cost-benefit model that carnivory would only be beneficial for plants growing in sunny, moist, and nutrient-poor habitats, in which the benefits of carnivory would equal or rather exceed the costs associated with carnivory. The model focused on enhanced photosynthesis as the primary physiological consequence and benefit of carnivory and made three predictions (see also Givnish, 1989; Ellison and Gotelli, 2001; Ellison, 2006, Guisande et al., 2007). First, carnivorous plants should have an energetic advantage in competing with non-carnivorous plants. Further, the primary energetic benefit of carnivory should be either an increased photosynthetic rate per unit leaf mass or total leaf mass supported. Finally, the absolute benefit of carnivory should saturate and the marginal benefit should decline with increasing investment in carnivory when factors other than nutrients (e.g. light, water) are limiting. The main structural and "nutrient" costs of carnivory are the production of traps. However, traps are also associated with photosynthetic and energetic (metabolic) costs. First, $P_{max}$ of traps is lower than that of leaves but the data are still scarce (Knight, 1992; Adamec, 1997b, 2006; Ellison and Gotelli, 2002; Pavlovič et al., 2007). Second, RD of traps (as maintenance cost), due to their intensive physiological processes, is much greater than that of non-carnivorous parts of the leaves (Knight, 1992; Adamec, 2006).

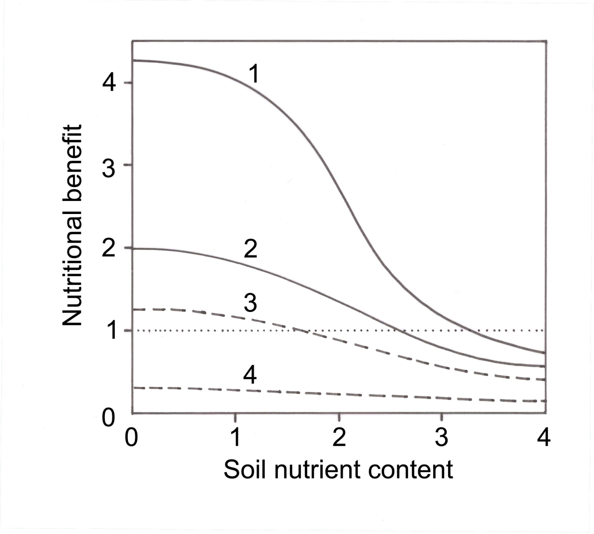
Although photosynthesis is a key process and prerequisite of plant growth, the focus of Givnish et al. (1984) on photosynthesis increase as a primary consequence and benefit of carnivory has probably been rather overestimated. As terrestrial carnivorous species being S-strategists are evolutionarily adapted to low RGR, the capacity to accelerate their growth is limited (Adamec, 2002, 2008d; Farnsworth and Ellison, 2008) and, thus, they do not require high $P_{max}$ per unit biomass. This conclusion clearly follows from the study by Shipley (2006) on close correlation of $P_{max}$ values with RGRs in plants. Moreover, on the basis of the fact that $P_{max}$ may not increase due to carnivory and owing to relatively low foliar N and P content in carnivorous plants (see 5.), it is possible to assume that slow growth of carnivorous plants is rather limited by a shortage of mineral nutrients necessary for growth processes in growing centers. Thus, the primary physiological benefit of carnivory could be to provide N and P for essential growth processes such as cell division, DNA replication, and proteosynthesis in young, miniature tissues in shoot apices (Adamec, 2008a) though the measurement of tissue N and P content in "bulk" shoot apices did not confirm this assumption (Adamec, 2000, 2008a). In this line, the primary physiological benefit of carnivory in terrestrial species could also be the stimulation of root nutrient uptake (see 6.).

Summarily, the ecological cost-benefit relationships of carnivory could therefore be expressed (instead of photosynthesis, Givnish et al., 1984) in the terms of *relative gain* of limiting mineral nutrients coming from carnivory (or *efficiency* of mineral nutrient investment in traps). All carnivorous plants have to invest some amount of mineral nutrients in the production of traps ($M_1$ for a given nutrient) within the growing season, which is a mineral nutrient cost of carnivory. A portion of this amount ($M_2$) is lost with the senescent biomass; the difference $M_1 – M_2$ is reutilized (see 6.). The traps containing $M_1$ mineral nutrients are able to gain a certain amount of mineral nutrients from prey ($M_3$) over their trap lifespan (a trap does not necessarily survive for an entire growing season). Assuming mineral nutrient uptake from prey to be the main *direct* ecophysiological benefit of carnivory, then the $M_3$:$M_2$ ratio characterizes the *direct* nutritional benefit (and also efficiency) of carnivory. It expresses how many atoms of e.g. N is taken up from prey per one atom of N lost with the senescent trap biomass, but not per the total trap N amount. However, to ignore the total trap nutrient amount ($M_1$) in the nutrient-based cost-benefit relationships of carnivory is a simplification as carnivorous plants must invest first this amount to trap production, although the reutilizable amount ($M_1 – M_2$) is not lost for the plant. Therefore, some differences in the interpretation of this model may occur among evergreen, temperate, and annual carnivorous species. Nevertheless, in terrestrial carnivorous species, a greater proportion of mineral nutrients gained as a result of carnivory is taken up by roots from the soil, as a result of the stimulation of root nutrient uptake (see 6.). Thus, the direct nutritional gain from prey ($M_3$) should be added to the amount of nutrients gained *indirectly* by the plant due to this root stimulation ($M_4$) as *indirect* ecophysiological benefit of carnivory. Then, the $M_4$:$M_2$ ratio characterizes the *indirect* nutritional benefit of carnivory, the sum $M_3 + M_4$ the *total* ecophysiological benefit of carnivory in the terms of nutrient gain, and, consequently, the expression $(M_3 + M_4)/M_2$ characterizes the *total* nutritional benefit of carnivory, as the sum of the *direct* and *indirect* nutritional benefits of carnivory (see Fig. 1). A simpler interpretation of these parameters might be for plants with traps distinctly separated from photosynthetic leaves (e.g. *Genlisea*, *Utricularia*) than for those with combined traps and leaves (e.g. *Drosera, Pinguicula*). Furthermore, it is possible to assume that, in mineral-richer soils, a greater proportion of all mineral nutrients to the total plant amount will be taken up by roots from the soil (or from the ambient water in aquatic species) and, thus, the nutritional contribution of carnivory will be declining sigmoidally below 1. The value of the total nutritional benefit equal to 1 denotes the level under which carnivory for a given nutrient is not ecologically beneficial.

As follows from this definition both the direct, indirect, and total nutritional benefits of carnivory are zero in carnivorous plants without any prey, however rapid their growth and nutrient uptake are. This must be respected at experimental estimations of these parameters: nutrient amounts in unfed controls should be subtracted from those in variants with prey (s*ensu* Hanslin and Karlsson, 1996; Adamec, 2002). So far, these parameters have not been presented and complete data for their calculation are lacking. Generally, there are two approaches to estimate or assess the nutritional benefits of carnivory. In all cases, for estimation of these parameters, the data on the proportion of trap nutrient amount (or at least DW) to the total plant one and on the efficiency of mineral nutrient reutilization from traps (leaves) are necessary. One approach to estimate both direct and indirect benefits is based on detailed data from a growth experiment on feeding on prey or supply of nutrient solution onto the traps (Hanslin and Karlsson, 1996; Adamec, 2002). To estimate the indirect nutritional benefit, presented values of “efficiency of the use of nutrients supplied onto the leaves” (Adamec, 2002) might also be used. Secondly, in natural populations of carnivorous plants, the estimated values of the proportion of seasonal nutrient gain from carnivory (see 7.2., Tab.1) together with the relationship between the seasonal nutrient gain and total plant nutrient amount may be used for assessing the direct nutritional benefit.

In mineral-poor soils, at high natural rates of prey capture, on the basis of known efficiencies of nutrient uptake from prey and nutrient reutilization (see 6.), and assuming the proportion of trap DW to the total one to be about 40% in *Drosera* spp. or 80% in *Pinguicula* spp., the total nutritional benefit of carnivory at high prey capture rates should be several units (2-10) for N, P, and K, around 1 for Mg, but only about 0.5 for Ca, while the direct values for all nutrients should be much lower (Fig. 1). The assessments of direct values for a growth experiment on three *Drosera* species fed on nutrient solution (Adamec, 2002) were about 0.4 for N, 0.2 K, 0.1 Mg, and 0.07 for Ca, while the total values were about 4.0 for N, 11 P, 5.5 K, 1.1 Mg, and 0.5 for Ca. Similarly, the experimental data on feeding three European *Pinguicula* species on fruit flies (Hanslin and Karlsson, 1996) may lead to an assessment of the direct values for N within 0.8-2.7, while the total ones within 1.7-7.0. *D. rotundifolia* and *D. intermedia* capture prey very efficiently and the covering 90% of their seasonal N and P gain and 1.5% K gain from carnivory (Table 1; Thum, 1988) may lead to the direct nutritional benefit of about 3.6 for N, 8.1 P, but only 0.08 for K. In aquatic *U. macrorhiza*, the total value of about 4.3 for N can be assessed from the study by Knight (1988).

To what extent does this model reflect reality? Obviously, this nutritional model may be useful in comparing and quantifying both the nutrient losses in senescent traps as the nutritional cost, and the direct and indirect nutrient gains as the benefits. The model confirms the experimentally-based results on that the direct mineral nutrient uptake from carnivory is usually several times lower than the indirect one due to root uptake stimulation and that this disproportion is relatively greater for K, Mg, and Ca than for N and P (see 6.; Adamec, 1997a, 2002; Hanslin and Karlsson, 1996). It follows clearly from the model that individual mineral nutrients taken up from carnivory differ greatly in their relative benefit for the plants: the nutrients taken up very efficiently from prey carcasses (N, P, K) and, simultaneously, being reutilized very efficiently from senescing leaves (N, P, K) are candidates for mineral nutrients which brought an ecological advantage for plants with this adaptation and evolutionarily supported carnivory. In contrast, Mg and Ca reutilization is usually very poor and also, due to their low tissue content in prey and zero Ca uptake from prey, direct uptake of these two nutrients from prey could not “drive” carnivorous plant evolution. Instead, to ensure the seasonal Ca and Mg gain by the plants and avoid thus a possible Ca- and Mg-based growth limitation, efficient physiological mechanisms were developed to stimulate Ca and Mg uptake by roots. In conclusion, to be nutritionally beneficial, carnivorous plants do not need only to capture prey efficiently (per trap biomass), but also to maximize nutrient uptake from prey and minimize nutrient losses in senescing traps. The fact that terrestrial carnivorous plants show a very efficient N, P, and K reutilization from shoots supports this concept. The “nutritional” concept of carnivory does not deny the outcomes of the photosynthetic concept (Givnish et al., 1984). Rather, it prefers the importance of mineral nutrients for carnivory.



**Legend to Fig. 1**
Schematic model for the nutritional benefits of carnivory as dependent on available soil mineral nutrient content (arbitrary units). Nutritional benefits in this scheme include either direct or total nutritional benefits (for their explanation see the text). 1, total nutritional benefit for N, P, and K, high prey capture; 2, total nutritional benefit for N, P, and K, low prey capture; 3, direct nutritional benefit for N and P and total nutritional benefit for Mg, high prey capture; 4, direct nutritional benefit for K, Ca, and Mg, high prey capture.

Overall, looking at worldwide species diversity of terrestrial carnivorous plants, it can be concluded that the majority of species (about 70-80%) do obey the ecological predictions given by Givnish et al. (1984) and grow more or less in sunny, moist, and nutrient-poor habitats (e.g. Juniper et al. 1989; Taylor, 1989; Rice, 2006; Studnička, 2006). However, the other terrestrial species can be considered facultatively (or even strictly) sciophilous (i.e. shade adapted) and grow within the herbal understorey under the canopy of taller accompanying vegetation (e.g. *Utricularia*, *Genlisea*, *Pinguicula*), or in shaded rocky walls (*Pinguicula*), or in tropical rainforests under a canopy of trees (*Nepenthes, Drosera, Triphyophyllum*). In contrast, *Drosophyllum lusitanicum* is an atypical xerophytic species (Adlassnig et al. 2006).

Within the ecological group of about 50 species of aquatic carnivorous plants (see 8.2.), the absence of sunny habitats is presumably much more common than in terrestrial ones as many aquatic *Utricularia* species can either be considered sciophilous or grow in rather shaded habitats or in dark waters (often <5% of incident irradiance; Adamec, 2008b). Yet, they are still carnivorous but, under shade conditions, they could reduce greatly their growth rate. However, when irradiance falls below a critical limit or $CO_2$ is under shortage their investment in trap production is minimal or zero (Bern, 1997; Englund and Harms, 2003; Adamec, 2008b). Generally, the above predictions on habitat requirements given by Givnish et al. (1984) should not be applied for aquatic carnivorous plants. Instead, it is possible to suggest that carnivory in aquatic environments will only be beneficial for plants in nutrient-poor and $CO_2$-rich habitats at above-threshold irradiance above 5-10% of that in the open.

## 10. Phylogeny of carnivorous plants: how many times in the history?

As follows convincingly from modern molecular-taxonomic studies, recent carnivorous plants evolved in 5-6 lineages from its preliminary ancestors (probably protocarnivorous plants; Spomer, 1999) independently on each other within evolution (i.e., polyphyletic origin; e.g. Müller et al., 2004; Heubl et al., 2006; Porembski and Barthlott, 2006). However, due to the lack of fossil material, the original ancestral types are still mostly unknown. For a long time, the paleaospecies *Palaeoaldrovanda splendens* from Late Cretaceous (75-85 mya; Degreef, 1997) was considered the oldest known carnivorous plant, representing the ancestral type of the recent *Aldrovanda vesiculosa*. Recently, a fossil angiosperm plant *Archaeamphora longicervia* has been described from the Early Cretaceous Yixian Formation (125 mya), NE China, as a possible ancestor of the modern *Sarraceniaceae* (Li, 2005). Morphologically, it resembles to *Sarracenia purpurea* and *Heliamphora* very much. Thus, it probably represents the oldest carnivorous plant and the only fossil record of pitcher plants. Assuming the age of Angiosperms to be about 280 mya (see Li, 2005), then these findings show that the origin of carnivorous plants was relatively very early in the evolution of Angiosperms. On the other hand, carnivory was lost secondarily in recent genera of the family Ancistrocladaceae and almost lost in Dioncophyllaceae (except *Triphyophyllum peltatum*; Heubl et al., 2006).

Within carnivorous plants, the greatest attention has recently been paid to studying the molecular-taxonomic and evolutionary relationships in Lentibulariaceae comprising about 325 species of three genera (e.g., Jobson et al. 2003; Müller et al., 2004, 2006; Laakkonen et al., 2006). In two genera of the rootless *Utricularia-Genlisea* clade, but not in *Pinguicula,* extremely high DNA mutation rates were found (Müller et al., 2004, 2006). This high mutation rate in *Utricularia* and *Genlisea* is associated with the smallest genome size in these two genera within Angiosperms (Greilhuber et al., 2006) and is explained as the metabolic consequence of direct uptake of organic substances (e.g. amino acids). Nevertheless, the rootless aquatic *Aldrovanda vesiculosa* (Droseraceae) has exactly the same type of mineral and organic nutrition as aquatic *Utricularia* species have (see 8.5., 8.6) but its DNA mutation rate is extremely low, and as such could be considered a “living fossil” (Maldonado San Martín et al., 2003; Hoshi et al., 2006). It seems, therefore, that the reasons for such a behavior will be elsewhere. In *Utricularia* (but not in *Genlisea*) species, a mutation in the mitochondrial cytochrome *c* oxidase has recently been found (Laakkonen et al., 2006). This mutation would permit the plants to increase energy output (for rapid trap movement), but with a 20% reduction in energy efficiency of the respiratory chain. On the basis of their model, the authors suggest that this mutation leading to greater RD could represent a metabolic benefit, was evolutionary advantageous, and could contribute to faster evolution of this genus.

## 11. Concluding remarks: inspiration for further research

As shown in the review, carnivorous plants have evolved several times during plant evolution independently on each other, mainly as an ecological adaptation to combination of mineral nutrient poverty in wet soils, usually in sunny habitats. Thus, there was a permanent and strong selective pressure in plant evolution to adapt to these stressful conditions. The main ecophysiological strategy of terrestrial carnivorous species as S-strategists is slow growth and very effective mineral nutrient economy. This strategy, together with gaining mineral nutrients from carnivory, does not require a high photosynthetic rate – as compared to non-carnivorous species – and enables them to survive even in very barren wet habitats. Following from the typical tissue mineral nutrient content in animal prey carcasses, it is N and P (partly also K) taken up from prey that are of the greatest importance for plant growth. The benefit of carnivory always depends on the quantity of captured prey so that successful “trappers“ can compensate from prey up to 60-100% of their seasonal N and P gain, but only 1-16% of K. Besides the direct mineral enrichment of carnivorous plants in nutrients coming from prey, foliar nutrient uptake from prey very markedly stimulates root nutrient uptake representing the main physiological effect of carnivory.

Aquatic carnivorous species are ecophysiologically quite dissimilar to their terrestrial counterparts. The principal growth traits in rootless aquatic species with linear shoots – very rapid apical shoot growth and high RGR even in barren habitats – are associated with very steep physiological polarity along the shoots and require a combination of several ecophysiological processes. They include the capture of animal prey, very high $P_{max}$, very efficient mineral nutrient uptake from water, and efficient mineral nutrient reutilization (except K) from senescent shoots.

Generally, it is possible to conclude that carnivory is *almost indispensable* for naturally growing carnivorous plants.

To obtain further insight into the ecophysiology of growth and nutrition of carnivorous plants, the following directions of research could be considered and the questions raised could be answered.

1. Basic properties of mineral ion uptake need to be studied in isolated roots, e.g. mineral nutrient uptake affinity and capacity for different mineral ions, and compared with those in roots of non-carnivorous plants.
2. The stimulation of root nutrient uptake by foliar uptake represents the main physiological effect of carnivory but its essence is still unknown. It is not known whether it is mediated by increased allocation of photosynthates or mineral nutrients from leaves to roots or whether it represents primary or secondary effects of utilization of prey.
3. The effect of growth enhancement due to carnivory: which physiological effects are primary and which are secondary? What is the role of tissue N and P content in this growth enhancement? If carnivory does not increase $P_N$ per unit shoot biomass, it is possible to assume that the positive growth effect is caused by stimulation of cell divisions in juvenile tissues in shoot apices.
4. Steep growth polarity in aquatic carnivorous plants and their very rapid apical shoot growth associated with the steep physiological polarity imply the involvement of

physiological processes which are insufficiently understood (e.g., phytohormone distribution).

5. In aquatic carnivorous plants, what is the affinity of shoots for mineral nutrient uptake from water? Is shoot nutrient uptake from the ambient water stimulated by prey capture (in analogy with terrestrial species)? What is the efficiency of mineral nutrient uptake from prey?
6. On the basis of the ecophysiological peculiarities of aquatic carnivorous plants, the cost-benefit model of carnivory needs to be elaborated for this particular plant group.
7. What is the role of organic nutrition in carnivory?
8. Food webs have been described in traps of many carnivorous plant species. What is the role of commensals living in the traps for nutrient uptake by plants?

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