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REVIEW

A novel insight into the cost–benefit model for the evolution of botanical carnivory

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• **Background** The cost–benefit model for the evolution of botanical carnivory provides a conceptual framework for interpreting a wide range of comparative and experimental studies on carnivorous plants. This model assumes that the modified leaves called traps represent a significant cost for the plant, and this cost is outweighed by the benefits from increased nutrient uptake from prey, in terms of enhancing the rate of photosynthesis per unit leaf mass or area (A_N) in the microsites inhabited by carnivorous plants.
• **Scope** This review summarizes results from the classical interpretation of the cost–benefit model for evolution of botanical carnivory and highlights the costs and benefits of active trapping mechanisms, including water pumping, electrical signalling and accumulation of jasmonates. Novel alternative sequestration strategies (utilization of leaf litter and faeces) in carnivorous plants are also discussed in the context of the cost–benefit model.
• **Conclusions** Traps of carnivorous plants have lower A_N than leaves, and the leaves have higher A_N after feeding. Prey digestion, water pumping and electrical signalling represent a significant carbon cost (as an increased rate of respiration, R_D) for carnivorous plants. On the other hand, jasmonate accumulation during the digestive period and reprogramming of gene expression from growth and photosynthesis to prey digestion optimizes enzyme production in comparison with constitutive secretion. This inducibility may have evolved as a cost-saving strategy beneficial for carnivorous plants. The similarities between plant defence mechanisms and botanical carnivory are highlighted.

Key words: Action potential, botanical carnivory, carnivorous plant, cost–benefit, *Dionaea*, *Drosera*, electrical signalling, jasmonates, *Nepenthes*, Venus flytrap.

INTRODUCTION

Carnivorous plants have long fascinated scientists, and were described by Charles Darwin in the book *Insectivorous plants* (Darwin, 1875). Carnivorous plants typically attract, capture and digest animal prey by modified leaves called traps. No carnivorous plant is able to capture prey by its flower. Givnish *et al*. (1984) proposed that a plant must fulfil two basic requirements to be considered as carnivorous. First, it must be able to absorb nutrients from dead prey, and thereby obtain some increment to fitness in terms of increased growth, pollen production or seed set. Secondly, the plant must have some adaptation or resource allocation whose primary result is the active attraction, capture and/or digestion of prey. The first is needed to differentiate carnivory from defensive adaptation that immobilizes or kills animal enemies without leading to substantial nutrient absorption and thus increased plant survival. The second is required because many plants can passively profit by absorbing some nutrients from dead animals decomposing in the soil or on leaf surfaces. A plant must have at least one adaptation (i.e. active attraction, capture and digestion) in combination with nutrient absorption to be qualified as carnivorous, because many genera of carnivorous plants lack some of these attributes. For example, *Utricularia* and *Pinguicula* probably lack resource allocation to prey attraction. *Heliamphora* and *Darlingtonia* lack digestive glands and enzymes (except probably *H. tatei*; Jaffé *et al*., 1992) and rely on symbiotic bacteria and other organisms to break down the prey (Adlassnig *et al*., 2011). The genus *Roridula* relies on a mutualistic relationship with *Pameridea roridulae*, a species of capsid bug, which lives on the plant and feeds on the trapped insects. The plant obtains nutrients from the droppings of this symbiotic insect (Anderson, 2005; Plachno *et al*., 2009). *Nepenthes bicalcarata* relies on the symbiotic ants *Camponotus schmitzi* to catch and digest its prey (Bonhomme *et al*., 2011*a*; Bazile *et al*., 2012; Thornham *et al*., 2012). These alternative methods of prey digestion, called digestive mutualisms, may represent extremely specialized adaptation to the carnivorous syndrome because they reduce the costs of having to produce digestive enzymes (Anderson and Midgley, 2003). According to this new definition, the plant *Paepalanthus bromelioides* is considered as a carnivorous plant (Nishii *et al*., 2013; Givnish *et al*., 2015).

Although 19 genera in 12 families and five orders of carnivorous plants are now recognized (*Aldrovanda*, *Brocchinia*, *Byblis*, *Catopsis*, *Cephalotus*, *Darlingtonia*, *Drosera*, *Drosophyllum*, *Dionaea*, *Genlisea*, *Heliamphora*, *Nepenthes*, *Paepalanthus*, *Philcoxia*, *Pinguicula*, *Roridula*, *Sarracenia*, *Triphyophyllum* and *Utricularia*; Givnish *et al*., 2015; Fig. 1), some authors argue that there are more carnivorous plant genera than previously believed and that there is a clear continuum

Fig. 1. The carnivorous plants. (A) *Cephalotus follicularis*, (B) *Darlingtonia californica*, (C) *Dionaea muscipula*, (D) *Nepenthes tentaculata*, (E) *Heliamphora nutans*, (F) *Sarracenia flava*, (G) *Drosera roraimae*, (H) *Pinguicula alpina*, (I) *Utricularia humboldtii*.

between carnivorous and non-carnivorous plants. Recently, Chase *et al*. (2009) discussed as carnivorous the sticky plants *Potentilla glandulosa*, *Geranium viscosissimum*, *Petunia violacea*, *Petunia nyctaginiflora* and *Solanum tuberosum*, and plants that use glandular hairs to protect their flowers, including *Stylidium* species, *Passiflora foetida* and *Plumbago auriculata*. They also included plants that make pitchers with their leaves including *Dipsacus fullonum*, plants that kill birds including *Puya raimondii*, and more. Although that paper attracted media attention, many authors disagree with such a broad definition of carnivorous plants, because they do not fulfil the above-mentioned criteria (Brittnacher, 2011; Rice, 2011).

A long-standing problem in evolutionary biology, i.e. an explanation for the ecological conditions under which botanical carnivory is likely to evolve repeatedly, was resolved by Givnish *et al*. (1984). Several comprehensive reviews of the rise of carnivorous plants have been published over the past decade, all focusing on trade-offs among physiological and morphological traits (Ellison and Gotelli, 2001, 2009; Ellison, 2006; Ellison and Adamec, 2011). Here, we review the cost–benefit model for the evolution of botanical carnivory in view of new data on the molecular biology of trap leaves. In addition to the classical ecological intepretations of that model, we highlight the importance of energetic costs of active trapping mechanisms. We also attempt to address the similarities between carnivory and plant defence mechanisms and the role of jasmonate signalling in carnivory. Finally, we extend the intepretation of the cost–benefit model to alternative nutrient sequestration strategies in carnivorous plants.

TRAPPING MECHANISMS

The traps of carnivorous plants may be active or passive, depending on whether movement aids the capture of prey. Five basic trapping mechanisms are found in carnivorous plants (Juniper *et al*., 1989; Król *et al*., 2012).

Pitfall traps (pitcher plants)

These trap prey into a modified pitcher that contains a pool of digestive enzymes or bacteria. Special adaptation such as wax layers, anisotropy of digestive glands, slippery peristome and acidic and viscoelastic digestive fluid are involved in the capture mechanism (Bohn and Federle, 2004; Gaume *et al*., 2004; Gorb *et al*., 2004; Gaume and Forterre, 2007; Bazile *et al*., 2015). Prey usually lose stability on slippery surfaces and fall inside the pitcher with digestive fluid. Passive pitfall traps are thought to have evolved six times independently in the families Sarraceniaceae (*Sarracenia*, *Heliamphora*, *Darlingtonia*), Cephalotaceae (*Cephalotus*), Nepenthaceae (*Nepenthes*) and Eriocaulaceae (*Paepalanthus*) and twice in the family Bromeliaceae (*Brocchinia* and *Catopsis*) (Givnish *et al*., 2015).

Flypaper traps

These traps involve a sticky mucilage on the leaf surface. Flypapers have evolved at least five times independently in the following genera: *Drosera* (family Droseraceae), *Drosophyllum* (family Drosophyllaceae), *Triphyophyllum* (family Dioncophyllaceae), *Byblis* (family Byblidaceae), *Pinguicula* (family Lentibulariaceae), *Roridula* (family Roridulaceae) and the recently described genus *Philcoxia* (family Plantaginaceae; Renner and Specht, 2011; Pereira *et al*., 2012; Givnish *et al*., 2015). Mucilage-secreting glands may be short (like those of the *Pinguicula*), or long and mobile (like those of *Drosera*). There are active and passive traps. For example, *Triphyophyllum* has a passive flypaper trap that secretes mucilage, but whose leaves do not move in response to prey capture. Sundew (*Drosera*) has active flypaper traps with tentacles and leaf bending reactions. A special category of tentacles has recently been described: fast-moving snap tentacles in *Drosera glanduligera* (Poppinga *et al*., 2012).

Snap traps

These traps utilize rapid leaf movements. There are only two closely related active snap trap genera – *Dionaea* and *Aldrovanda* (family Droseraceae). The rapid trap closure is triggered by action potentials generated by touch of sensitive hairs on the trap lobes (Volkov *et al*., 2008).

Bladder suction traps

These suck in prey with a bladder that generates an internal vacuum and are exclusively found in the genus *Utricularia* (family Lentibulariaceae). The bladders actively pump ions out of their interiors and water follows by osmosis; this generates a partial vacuum inside the bladder. Aquatic invertebrates touch the trigger hairs and deform the door by lever action, releasing the trap wall and causing water influx. The invertebrate is sucked into the bladder, where it is digested (Vincent *et al*., 2011*a*, *b*; Adamec, 2012).

Eel-traps

These traps force prey to move towards a digestive organ with inward-pointing hairs. These are passive traps. They are found in the genus *Genlisea* (family Lentibulariaceae) and in *Sarracenia psittacina* (family Sarraceniaceae) (Adamec, 2003).

COST–BENEFIT MODEL FOR EVOLUTION OF BOTANICAL CARNIVORY

Today >650 species of carnivorous plants have been recognized, including monocotyledons and eudicotyledons (Ellison and Adamec, 2011). They have evolved at least nine times independently and are thus an example of convergent evolution (Albert *et al*., 1992; Givnish *et al*., 2015). Recently, the first fossilized (35–47 milion years old) carnivorous plant trap of the family Roridulaceae was found (Sadowski *et al*., 2015). Convergent evolution is an independent evolution of similar features in species of different lineages which grow or live in a similar environment. For example, pitcher plants *Sarracenia* and *Nepenthes* are not related and pitcher traps are analogous, not homologous, structures (i.e. they have not evolved from a common ancestor). What environmental factors are the driving forces for evolution of botanical carnivory? Ecologist Thomas Givnish was the first to recognize why carnivorous plants are mainly restricted to habitats and microsites that are not only nutrient poor, but sunny and moist as well. In January 1980, Thomas Givnish visited the Gran Sabana in Venezuela, where he observed terrestrial bromeliad *Brocchinia reducta*. He noticed that this bromeliad has evolved some features which resembled a carnivorous lifestyle. In contrast to related species such as *B. tatei*, *B. reducta* forms bright yellow-green leaves which are held vertically enclosing its own water tank. The fluid inside the tank is highly acidic (pH 2.8–3.0) and contains abundant remains of dead insects. The tank emits a sweet odour. The leaf surface is coated with a fine waxy layer inhibiting prey escape from the central tank. After removing this layer by brushing, attempts by ants to ascend the leaf surface succeeded. Finally, the trichomes of *B. reducta* can absorb ^{3}H-labelled leucine. Based on the criteria mentioned above, *B. reducta* fulfils all the requirements to be classified as carnivorous. Although the evidence that absorption of nutrients increases *B. reducta* fitness is missing, it is very likely that it occurs, because it grows in a nutrient-poor habitat that is the home of other genera of carnivorous plants (*Drosera*, *Heliamphora*, *Genlisea* and *Utricularia*), where benefit from prey capture in terms of increased growth was documented (Ellison, 2006). Givnish *et al*. (1984, 1997) also proposed possible mechanisms for how the carnivory in *B. reducta* may have evolved. The closest relative of *B. reducta* is *B. tatei*, which is a facultatively epiphytic tank species growing in shady cloud forest. Its nearly horizontal rosette-forming green leaves are well adapted for light capture (Fig. 2). The leaves of *B. tatei* form a spreading rosette and capture moderate amounts of

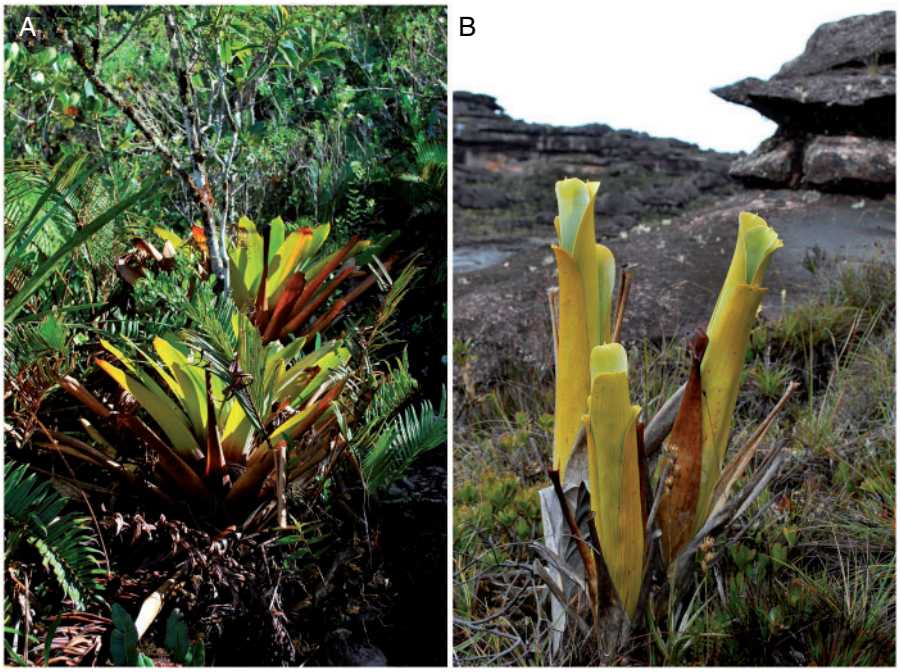

FIG. 2. Two related species of *Brocchinia* growing in the Guiana Highlands, Venezuela. (A) The non-carnivorous species *Brocchinia tatei* often grows in cloud forest and forms nearly horizontal rosette-forming green leaves. (B) The carnivorous species *Brocchinia reducta* grows in open vegetation and forms bright yellow-green leaves which are held vertically.

precipitation and leaf litter in their bases. Under such conditions, it probably obtains some nutrients from the breakdown of such debris, like many other tank epiphytes. Invasion of sunny sterile savannah by *B. reducta*'s ancestors would have favoured the evolution of steeply inclined leaves with strongly reflective waxy cuticles to reduce light capture. These traits would be a pre-adaptation for the evolution of carnivory. The crucial shift to carnivory probably involved the leakage into the tank of a volatile compound stored in the leaf base of many *Brocchinia* species. This would attract insects into the tank and promote the evolution of other carnivorous-related functions. Thus *B. reducta* was the first documented case of carnivory in Bromeliaceae and even in monocotyledons. The related species *B. hectioides* also growing on Gran Sabana in Venezuela is considered as the second carnivorous species in the genus *Brocchinia*. It has evolved traits very similar to those of *B. reducta*. The third species is probably *Catopsis berteroniana*, but more research on this species is needed (Frank and O'Meara, 1984; Givnish *et al*., 1984; Givnish, 1989). The fact that the genus *Brocchinia* also possesses other specialized adaptations to nutrient capture (myrmecophytic *B. accuminata*, nitrogen (N) fixation in some populations of *B. tatei*) in nutrient-poor habitats indicates that they have evolved in the process of adaptive radiation. Givnish *et al*. (1997) hypothesized that the tank habit and absorptive trichomes are the two key innovations that allowed the evolution of a great diversity of specialized mechanisms of nutrient capture including carnivory.

The observations of Givnish in Gran Sabana in Venezuela led him to formulate a cost–benefit model for evolution of botanical carnivory. Cost–benefit models have been a hallmark of ecological analyses for >50 years, and ask what organismal form, physiology or behaviour would maximize energy capture in a particular environment and thus be likely to result in maximal competitive ability and fitness in that context. The amount of energy a given organism can allocate to different functions is fixed, so that there are inevitably trade-offs among allocations to those functions, with the optimal allocation almost certainly varying with environmental conditions. In other words, it is based on the assumption that organisms cannot do equally well and there must be some trade-off. Carnivorous plants are model systems for studying a wide range of ecophysiological and ecological processes, and the application of a cost–benefit model for the evolution of carnivory by plants has provided many novel insights. Carnivory should evolve if benefits from increased uptake of nutrients from animal prey exceed the cost of investment in carnivorous adaptations. In this case, the plants obtain an advantage in competing with other plants in nutrient-poor habitats. Givnish *et al*. (1984) considered that the costs of carnivory included the extra energy required to attract prey (e.g. production of lures), capture prey (e.g. production of wax or mucilage) and digest prey (e.g. production of digestive enzymes), as well as a decreased rate of photosynthesis per unit leaf mass or area (A_N). Against these, he proposed three potential benefits from carnivory:

1. Carnivory may increase a plant's A_N through improved nutrient supply, particularly N status, in two ways: either by increased A_N per unit leaf mass or by an increase in the total leaf mass that can be supported.
2. Carnivory may result in an increased seed production through improved mineral acquisition.
3. Carnivory may replace autotrophy partly by heterotrophy.

Givnish *et al*. (1984) considered the second benefit as a part of the first, as increased A_N should lead to increased seed

production, and the third benefit as unlikely, because experimental evidence supports the fact that carnivorous plants obtain minerals, not carbon. He concluded that the primary benefit from carnivory is increased A_N through increased nutrient supply from prey. However, the A_N does not increase equally well under all conditions. If the factors such as light or water are in short supply and limit photosynthesis, then A_N increases more slowly with improved N content than at high light or high water supply, because of light and stomatal limitation of photosynthesis. It is known that carnivorous plants give up carnivory temporarily if they grow in nutrient-rich soil or they do not have enough water and light. For example, the genera *Nepenthes* and *Cephalotus* stop producing their pitchers, *Sarracenia* forms non-carnivorous phyllodia instead of traps, *Dionaea* decreases excitability of their trap, and *Drosera* and *Pinguicula* decrease the stickness of their leaves (Zamora *et al*., 1998; Ellison and Gotelli, 2002; Thorén *et al*., 2003; Pavlovič *et al*., 2010*b*; Escalante-Pérez *et al*., 2011). Thus, in summary, obviously where there is a shortage of nutrients and enough water and light, there is the greatest impact on photosynthetic gains from prey capture, and such conditions favour the evolution of plant carnivory (see fig. 3 in Pavlovič *et al*., 2009). In contrast, the costs to carnivory are thought to exceed the benefits in shady, nutrient-rich and dry habitats, and carnivory has no adaptive value in such an environment and does not pay off. Thus the main outcome from the cost–benefit model, that energetic benefits of carnivory are likely to exceed its costs only in sunny, moist and nutrient-poor environments, became a framework for studies in carnivorous plants (Ellison and Gotelli, 2009).

When Givnish proposed the cost–benefit model for the evolution of botanical carnivory 30 years ago, there was almost no compelling evidence bearing on whether his intepretation was right or wrong. Although Darwin's son was the first who showed that the growth of the carnivorous plant *Drosera rotundifolia* was enhanced by insect feeding (Darwin, 1878), the final experimental proof that carnivory may enhance A_N was missing for another 130 years. The first study performed by Méndez and Karlsson (1999) did not show enhanced A_N in response to feeding in *Pinguicula vulgaris* probably due to the short feeding period. The study of Ellison and Gotelli (2002) showed that *Sarracenia purpurea* responded to nutrient addition by shifting from production of carnivorous pitchers to production of more photosynthetically active phyllodia. However, Wakefield *et al*. (2005) measured the A_N after feeding in the same species with prey but he did not find any increase of A_N. Later Ellison and Farnsworth (2005) showed that A_N correlated with foliar N content in *Darlingtonia californica* from different sites. Ellison (2006) summarized data from 24 studies, and his meta-analysis showed that there is a significant positive effect of prey addition on carnivorous plant growth, but data regarding photosynthesis are still lacking. The first experimental evidence that A_N increased in response to carnivory was documented at almost the same time in ten *Sarracenia* species (Farnsworth and Ellison, 2008), *Utricularia australis* (Adamec, 2008) and *Nepenthes talangensis* (Pavlovič *et al*., 2009). Later, the positive effect of feeding on A_N was found in *Nepenthes ampullaria* (Pavlovič *et al*., 2011*b*), *Nepenthes alata* (He and Zain, 2012), *Drosera capensis* (Pavlovič *et al*., 2014) and *Dionaea muscipula* (Kruse *et al*., 2014). In many of these studies the increase in A_N correlated well with the increased leaf N and/or phosphorus (P) concentrations and increased growth. The chlorophyll concentration also increased in response to feeding and it is the most sensitive indicator of nutrient stress in carnivorous plants (Moran and Moran, 1998; Farnsworth and Ellison, 2008; Pavlovič *et al*., 2009, 2011*b*, 2014; Bazile *et al*., 2012; He and Zain, 2012). Moreover, Adamec (1997, 2002) suggested that absorption of leaf mineral nutrients from prey stimulates root nutrient uptake. Nutrients taken up by the roots can enhance A_N and thus increase the benefit from carnivory in *Nepenthes talangensis* (Pavlovič *et al*., 2010*b*), indicating a high capacity for root nutrient uptake in some carnivorous plants (Gao *et al*., 2015). Increased flowering frequency and seed production as a secondary benefit from carnivory is also documented in carnivorous plants (Karlsson and Pate, 1992; Thorén and Karlsson, 1998; Pavlovič *et al*., 2009).

All these photosynthetic studies however showed another important thing: the A_N and photosynthetic nitrogen use efficiency (PNUE) in terrestrial carnivorous plants are lower than those in non-carnivorous plants, including graminoids, forbs, and deciduous and evergreen trees and shrubs. This documents the cost of carnivory in terms of a decreased rate of A_N (decreased A_N in traps) and in terms of the physiological consequences of slow growth and conditions of extremely low nutrient availability (decreased A_N in photosynthetic lamina; Mendéz and Karlsson, 1999; Ellison and Farnsworth, 2005; Ellison, 2006; Ellison and Adamec, 2011). Although the construction costs (the amount of glucose required to synthesize 1 g of carbon skeleton/biomass) of traps are not higher than the construction costs of, for example, roots or leaves, the low A_N results in long pay-back times (the time that a leaf needs to photosynthesize in order to recover the carbon investment used in its construction; Osunkoya *et al*., 2008; Karagatzides and Ellison, 2009). However, the construction costs do not include only construction of trap organs. Many carnivorous plants secrete sugar- (carbon) rich exudates. The mucilage of *Drosera capensis* comprises L-arabinose, D-xylose, D-galactose, D-mannose and D-glucuronic acid (Gowda *et al*., 1983). Also, the viscoelastic digestive fluid and waxy zone of the trap in the genus *Nepenthes* is composed of long-chain polysaccharides and aldehydes, respectively (Riedel *et al*., 2003; Bonhomme *et al*., 2011*b*). Similarly, rootless *Utricularia* plants supply easily available organic carbon (glucose, fructose and lactate) from photosynthesis to the microbial community thriving within the trap environment while benefiting from its by-products (Sirová *et al*., 2010, 2011). The traps of carnivorous plants are therefore probably more costly than was previously thought (Osunkoya *et al*., 2008).

From a morphological point of view, two types of carnivorous plants can be distinguished. Butterworts (*Pinguicula*), sundews (*Drosera*) and American pitcher plants (*Heliamphora* and *Darlingtonia*) have leaves that can both photosynthesize and capture prey. The Australian pitcher plant (*Cephalotus*), Venus flytrap (*Dionaea*), bladderworts (*Utricularia*), North American pitcher plants (*Sarracenia*), corkscrew plants (*Genlisea*) or Asian pitcher plants (*Nepenthes*) produce leaves that can photosynthesize but do not capture prey (photosynthetic laminae or phyllodes), and/or produce traps that capture prey and photosynthesize little or not at all (Ellison and Gotelli, 2001). This trait allows them to vary their investment in carnivory as a function of environmental conditions (light, water and nutrient availability *sensu stricto* Givnish's cost–benefit model;

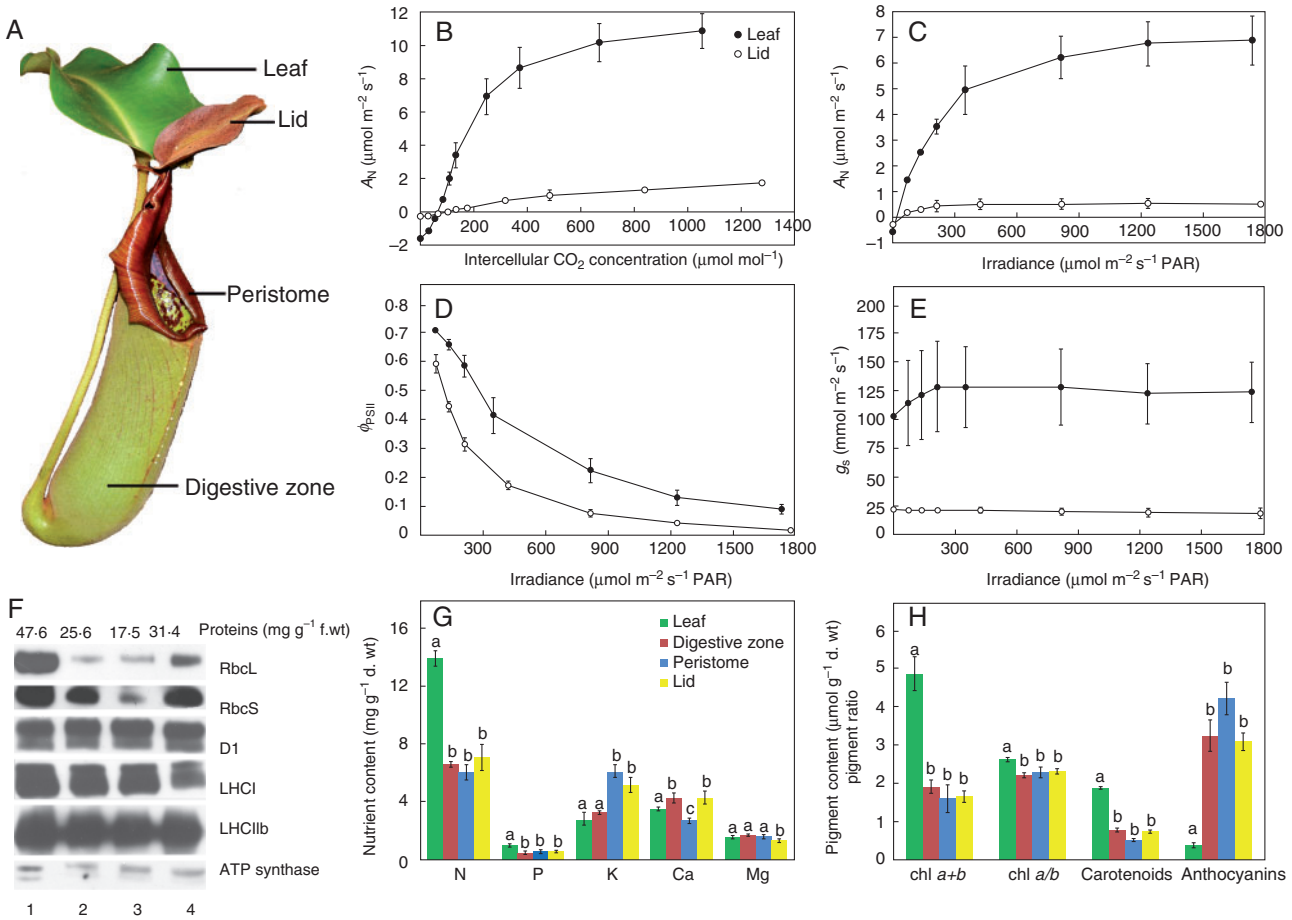

FIG. 3. Classical interpretation of the cost–benefit model for evolution of botanical carnivory in the genus *Nepenthes*. Comparison of photosynthetic characteristics between the pitcher (the lid as a flat part of the pitcher) and lamina. (A) The leaf of *Nepenthes truncata*. (B) *A*/*C*i response curve of photosynthesis. (C) Light response curve of photosynthesis. (D) Light response curve of effective photochemical quantum yield of photosystem II (ϕ_{PSII}). (E) Stomatal conductance (g_s). (F) Protein content and protein gel blot analysis (the same amount of protein was electrophoresed), leaf (1), digestive zone (2), peristome (3), lid (4). (G) Elemental composition of the leaf. (H) Pigment content and ratio. Data are means ± s.e. ($n = 5$); different letters denote significant differences among plant tissues (one-way ANOVA followed by Tukey's test). For details of the methods, see the Supplementary Data.

Knight and Frost, 1991). These plants are suitable models for cost–benefit studies, because reworking leaf morphology and physiology to carnivory apparently reduces the efficiency of A_N in traps. Pavlovič *et al.* (2007, 2009) compared A_N in the *Nepenthes alata*, *N. mirabilis* and *N. talangensis* lamina/leaf and pitcher trap separately and described the traits responsible for the carnivorous syndrome. This is briefly summarized in Fig. 3, here in the case of *Nepenthes truncata* (Fig. 3A). The traps of *Nepenthes* have very low A_N (close to zero), lower effective photochemical quantum yield of photosystem II (ϕ_{PSII}) and apparent quantum yield of CO_2 fixation (ϕ_{CO2}, slope of the linear portion of the light response curve, 0·019 ± 0·0019 and 0·003 ± 0·0006 mol CO_2 mol photons^{-1} for leaf and pitcher lid conditions, respectively), low stomatal density and conductance for CO_2 and H_2O (g_s), compact mesophyll without palisade parenchyma, and lower chlorophyll and carotenoid content but higher anthocyanin content (Fig. 3B–E, H). The pitchers, in comparison with photosynthetic leaves, also have a decreased amount of N and P (Fig. 3G). The pitchers also have lower protein content and a decreased amount of total soluble proteins invested in the Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase) large and small subunits, RbcL and RbcS, respectively, but almost the same invested in the chlorophyll-binding proteins (D1, LHCI and LHCIIb; Fig. 3F). This is consistent with decreased apparent Rubisco activity (ε) in the pitcher trap expressed as the slope of the linear part of the A/C_i response curve (0·44 ± 0·04 and 0·03 ± 0·005 μmol CO_2 m^{-2} s^{-1} Pa^{-1} for leaf and pitcher lid, respectively; Fig. 3B). In the prey-deprived plants of *N. ampullaria*, where the N concentration in leaves and traps was <0·5 %, the Rubisco content was almost comparable between the lamina and pitcher trap, making it tempting to assume that surplus N from prey is incorporated into Rubisco in the leaves, which may explain the higher A_N in fed plants (Pavlovič *et al.*, 2009, 2011*b*), an original hypothesis of Givnish *et al.* (1984). Rubisco is present at very high levels in photosynthesizing cells of C_3 plants and may contribute up to 50 % of soluble leaf proteins and 20–30 % of total leaf N (Feller *et al.*, 2008). Therefore, the photosynthetic capacity of leaves is related to the N content, and the proportion of total N in Rubisco increases with increasing leaf N (Evans, 1989). Recently, Galmés *et al.* (2014) characterized the kinetic properties of Rubisco from 28 terrestrial plant species, representing

different phylogenetic lineages, environmental adaptations and photosynthetic mechanisms, and found that carnivorous plants incorporated less total soluble proteins into Rubisco than non-carnivorous plants. As a result of extremely low protein incorporation into Rubisco, the Rubisco in carnivorous plants has evolved toward a higher maximum carboxylation rate. The higher maximum carboxylation rate probably does not compensate for lower protein investment in Rubisco, which may explain the lower PNUE in carnivorous plants. It seems that oxygen evolution (He and Zain, 2012) and electron transport from water (expresssed as ϕ_{PSII}) are not reduced to such an extent as dark enzymatic reactions of photosynthesis (compare the differences between the trap and lamina in A_N and ϕ_{PSII} in Fig. 3B–D, F), indicating that electrons from water are probably used in traps for competing processes other than photosynthesis. Pavlovič *et al*. (2007) predicted that the above-mentioned characteristics, which make photosynthesis in traps inefficient, may be responsible for the carnivorous function in nutrient-poor habitats (e.g. compact anatomy might serve for symplastic transport of nutrients gained from prey, N and carbon skeleton are allocated more into digestive fluid, enzymes and lures than to photosynthesis-related proteins).

A very low A_N and chlorophyll content were also found in the bladders in comparison with leaves of aquatic *Utricularia* by Knight (1992) and Adamec (2006). Although nobody has studied the genus *Genlisea*, it is almost certain that its colourless traps also have very low A_N if any. Thus, it is not surprising that such strongly modified leaves almost without photosynthetic activity are usually buried in substrate. Underground they can target a different type of prey, thus avoiding competition with sympatric terrestrial carnivorous plants. However, some other carnivorous genera have traps with not such drastically reduced A_N. For example pitchers of *Cephalotus*, *Sarracenia* or *Darlingtonia* have A_N almost comparable with the photosynthetic efficiency of assimilatory lamina (Ellison and Farnsworth, 2005; Farnsworth and Ellison, 2008; Hájek and Adamec, 2010; Pavlovič, 2011; Table 1). This indicates that some species indeed have reduced photosynthetic capacity in the trap organs (*Nepenthes*, *Utricularia*), but in others the A_N in the trap is only slightly, if at all, reduced in comparison with photosynthetic lamina (e.g. *Sarracenia*, *Cephalotus*, *Dionaea*), but is still very low in comparison with non-carnivorous plants (Méndez and Karlsson, 1999; Ellison and Farnsworth, 2005; Table 1). Altogether, these studies unequivocally showed that there is a photosynthetic cost in producing the traps in that the carbon invested in the traps does not return as much carbon as it would if it was invested in assimilatory tissue. As a result of our analyses, there is compelling evidence that traps have lower A_N than leaves (16 out of 18 cases), and that plants have higher A_N after feeding (16 out of 19 cases; Table 1).

Carbon uptake from prey considered as the third benefit from carnivory is negligible in terrestrial carnivorous plants, but is ecologically important for aquatic carnivorous plants (see Adamec, 1997). Although some studies have documented the uptake of carbon from prey in *Drosera erythrorhiza*, *Nepenthes insignis* or *Dionaea muscipula*, this absorbed carbon seems more likely to be in N-bearing amino acids than in carbohydrates (Dixon *et al*., 1980; Rischer *et al*., 2002; Kruse *et al*., 2014). Chandler and Anderson (1976) have shown that growth of dark-grown *Drosera whittakeri* was not enhanced in response to feeding, confirming the suggestion that carnivory cannot replace autotrophy by heterotrophy. This is in contrast to plants with a heterotrophic mode of nutrition (e.g. parasitic plants). Although the major source of the carbon skeleton in carnivorous plants is photosynthesis, recently the loss of genes, accelerated substitution rates and relaxation of selection in plastid genomes of *Utricularia*, *Genlisea* and *Pinguicula* were documented in comparison with non-carnivorous plants. Almost all genes for light and dark reactions of photosynthesis are affected and resemble the obligate photosynthetic parasitic plants such as *Cuscuta*, indicating that alternative paths of acquiring nutrients may promote the rapid evolution of plastid genes in Lentibulariaceae or in carnivorous plants in general (Revill *et al*., 2005; Wicke *et al*., 2014).

WATER PUMPING AND ELECTRICAL SIGNALLING

There is now a significant amount of evidence that the cost–benefit model proposed by Givnish *et al*. (1984) is valid for terrestrial carnivorous plants with slight modifications for aquatic carnivorous plants. Ellison and Adamec (2011) suggested that nutrient limitation is more pronounced in terrestrial carnivorous plants, which also have much lower growth rates and lower A_N than aquatic carnivorous plants. Because traps of aquatic carnivorous plants are energetically very costly, it is plausible that P limitation (of, for example, ATP) might be of more consequence for aquatic than for terrestrial carnivorous plants. As demonstrated by Sydenham and Findlay (1975), ions and water pumping during the resetting of *Utricularia* bladders is a process requiring high amounts of metabolic energy derived from aerobic respiration. When trigger hairs situated on trap door are touched by a prey, the door opens, prey is aspirated into the trap lumen and the watertight door closes again with a speed of 5 ms. In contrast to the Venus flytrap, this process has a purely mechanical basis, as electrical signals have never been recorded in *Utricularia* (Vincent *et al*., 2011*a*, *b*; Adamec, 2012). The first attempt to include respiratory cost in the cost–benefit model was made by Knight (1992), who found at least a 10 % greater respiration rate (R_D) in *Utricularia* bladders than in leaves. Adamec (2006) showed that R_D in *Utricularia* after firing and during resetting the bladders is even 75–200 % greater than in the leaves (Table 2). This results in anoxia inside the bladders within 30 min after trap firing and causes captured prey to die of suffocation (Adamec, 2007, 2010*b*). These findings led Laakkonen *et al*. (2006) to modify the cost–benefit model including respiratory costs as an additional trade-off parameter. Jobson *et al*. (2004) documented that the rate-limiting enzyme in the cellular respiration pathway, cytochrome *c* oxidase subunit I (COX I), may be functionally altered in bladderworts. They sequenced an intron-containing gene for 21 *Utricularia* species and identified that the otherwise conserved Leu113–Ser114 motif in COX I is replaced by Cys113–Cys114 across all examined *Utricularia* and some *Genlisea* species. No other carnivorous plant families have the motif, and neither does it appear in any other of the >30 000 COX I sequences currently databased for eukaryotes (with one exception – *Welwitschia mirabilis*). This motif lies directly at the docking point of COX I helix 3 and cytochrome *c*. The authors

TABLE 1. *Rate of net photosynthesis (A_N) in carnivorous plants with leaves differentiated into traps and photosynthetic lamina or in response to experimental feeding (fed plants in parentheses)*

Species (and reference)	Leaf type	A_N (nmol CO_2 g^{-1} d. wt s^{-1}) or A_{Naq} (mmol O_2 kg^{-1} f. wt h^{-1})	A_N (μmol CO_2 m^{-2} s^{-1})	Lower A_N in trap	Higher A_N after feeding
Aldrovanda vesiculosa (aq) (Adamec, 2008)	Shoot	34·1 ± 1·5 (21·5 ± 2·2)		N/A	–
Cephalotus follicularis (Pavlovič, 2011)	Lamina	42·8 ± 2·1		+	N/A
	Trap	27·2 ± 2·5			
Dionaea muscipula (Hájek and Adamec, 2010)	Lamina	90 ± 9	4·03 ± 0·38	+	N/A
	Trap	52 ± 3	3·04 ± 0·20		
Dionaea muscipula (Kruse *et al*., 2014)	Trap	Approx. 25 (approx. 38)		N/A	+
Drosera capensis (Pavlovič *et al*., 2014)	Trap		2·18 ± 0·52 (4·88 ± 0·57)	N/A	+
Nepenthes alata (Pavlovič *et al*., 2007)	Lamina	42·3 ± 4·5		+	N/A
	Trap	–2·4 ± 1·4			
Nepenthes alata (He and Zain, 2012)	Lamina		Approx. 4 (approx. 6)*	+	+
	Trap		Approx. 1 (approx. 2)*		
Nepenthes ampullaria (Pavlovič *et al*., 2011*b*)	Lamina		2·51 ± 0·55 (3·38 ± 0·37)	+	+
	Trap		0·07 ± 0·01 (0·20 ± 0·01)		
Nepenthes × *Coccinea* (Karagatzides and Ellison, 2009)	Lamina	29·8 ± 23·1 (s.d.)		+	N/A
	Trap	2·5			
Nepenthes mirabilis (Pavlovič *et al*., 2007)	Lamina	24·4 ± 5·5		+	N/A
	Trap	0·0 ± 1·6			
Nepenthes × *Miranda* (Karagatzides and Ellison, 2009)	Lamina	36·0		+	N/A
	Trap	1·1			
Nepenthes talangensis (Pavlovič *et al*., 2009)	Lamina	19·4 ± 2·0 (37·8 ± 5·4)	3·1 ± 0·3 (6·0 ± 0·5)	+	+
	Trap	2·0 ± 0·9 (3·5 ± 1·4)	0·10 ± 0·04 (0·15 ± 0·03)		
Pinguicula vulgaris (Méndez and Karlsson, 1999)	Plant	55·6 ± 16·9 (s.d.) (52·1 ± 10·0) (s.d)	2·2 ± 0·6 (s.d.) (2·2 ± 0·4) (s.d.)	N/A	0
Sarracenia spp. (ten species) (Farnsworth and Ellison, 2008)	Trap	Approx. 22 (38–45)		N/A	+ (10×)
Sarracenia flava (Karagatzides and Ellison, 2009)	Lamina	45·5 ± 7·3. (s.d.)		0	N/A
	Trap	43·0 ± 10·1 (s.d.)			
Sarracenia leucophylla (Karagatzides and Ellison, 2009)	Lamina	35·8 ± 24·1 (s.d.)		0	N/A
	Trap	36·5 ± 10·1 (s.d.)			
Sarracenia purpurea (Hájek and Adamec, 2010)	Wing	64 ± 6	5·26 ± 0·46	N/A	N/A
	Trap	58 ± 3	3·97 ± 0·22		
Sarracenia purpurea (Wakefield *et al*., 2005)	Trap		3·1 ± 1·2 (s.d.) (3·1 ± 1·2) (s.d.)	N/A	0
Utricularia australis (aq) (Adamec, 2008)	Leaf	66·7 ± 1·6 (89·2 ± 3·7)		N/A	+
Utricularia australis (aq) (Adamec, 2006)	Leaf	86·5 ± 10·1		+	N/A
	Trap	9·03 ± 1·22			
Utricularia bremii (aq) (Adamec, 2006)	Leaf	40·0 ± 6·6		+	N/A
	Trap	5·24 ± 0·51			
Utricularia floridana (aq) (Adamec, 2006)	Leaf	66·4 ± 3·9		+	N/A
	Trap	–5·09 ± 0·33†			
Utricularia intermedia (aq) (Adamec, 2006)	Leaf	117 ± 13·1		+	N/A
	Trap	–6·77 ± 0·57†			
Utricularia macrorhiza (aq) (Knight, 1992)	Leaf	0·758–0·965‡		+	N/A
	Trap	0·328–0·558‡			
Utricularia ochroleuca (aq) (Adamec, 2006)	Leaf	111 ± 5·6		+	N/A
	Trap	–5·15 ± 0·42†			
Utricularia vulgaris (aq) (Adamec, 2006)	Leaf	96·9 ± 5·2		+	N/A
	Trap	14·7 ± 0·64			
Summary				(+) 16 (–) 0 (0) 2	(+) 16 (–) 1 (0) 2

A positive response is indicated by '+', a negative response by '–', no response by '0', no data by 'N/A'.
Note the different unit for aquatic carnivorous plants (A_{Naq}).
Means ± s.e. whenever possible (or s.d. if indicated).
*Values are in μmol O_2 m^{-2} s^{-1}
†The traps are achlorophyllous; a negative sign of the number indicates CO_2 release (i.e. R_D).
‡Values are in mg C g $tissue^{-1}$ h^{-1}; values are from a population in Grassy Lake.

suggested two possible implications for such a substitution. The first is that a disulphide bridge at the bladderwort C–C motif could lead to early termination of helix 3 and decrease the surface area for cytochrome *c* association–dissociation and upregulate COX I kinetics. The second is that early termination of helix 3 leads to uncoupling of proton pumping from electron transport. Such decoupling would permit bladderworts to optimize power output during times of needs, although with a 20 % decrease in total energy efficiency of respiration. Moreover, Ibarra-Laclette *et al*. (2011) have recently found that bladders overexpress genes involved in respiration in comparison with leaves. Considering a higher R_D, they also found a higher rate of reactive oxygen species (ROS) production, which may be responsible for high elevated nucleotide substitution rates in the *Utricularia* organellar and nuclear genome and the dynamic evolution of genome size (but questioned by Wicke *et al*., 2014). The physiological data with some molecular support confirmed that the bladders of *Utricularia* are expensive structures due to their high R_D/A_N ratio (Ellison and Adamec, 2011).

TABLE 2. *Rate of dark respiration (R_D) in carnivorous plants with leaves differentiated into traps and photosynthetic laminae or in response to experimental feeding (fed plants in parentheses)*

Species (and reference)	Leaf type	R_D (nmol CO_2 g^{-1} d. wt s^{-1}) or R_{Daq} (mmol O_2 kg^{-1} f. wt h^{-1})	R_D (μmol CO_2 m^{-2} s^{-1})	Higher R_D in traps	Higher R_D after feeding
Aldrovanda vesiculosa (aq) (Adamec, 2008)	Shoot	8·17 ± 0·81 (8·97 ± 0·72)		N/A	0
Cephalotus follicularis (Pavlovič, 2011)	Lamina	3·48 ± 0·46		0	N/A
	Trap	2·97 ± 0·66			
Cephalotus follicularis (Adamec, 2010*a*)	Lamina	4·26 ± 0·25*		–	N/A
	Trap	2·22 ± 0·26*			
Dionaea muscipula (Adamec, 2010*a*)	Lamina	12·3 ± 1·2*		0	N/A
	Trap	14·2 ± 2·0*			
Dionaea muscipula (Hájek and Adamec, 2010)	Lamina	8·2 ± 1·8		0	N/A
	Trap	6·8 ± 0·6			
Dionaea muscipula (Pavlovič *et al*., 2010*a*)	Lamina		Approx. 0·3	+†	N/A
	Trap		Approx. 3·3		
Dionaea muscipula (Kruse *et al*., 2014)	Trap	Approx. 4·5 (approx. 8·5/4·5) (during/after feeding)		N/A	+/0 (during/after feeding)
Drosera capensis (Adamec, 2010*a*)	Lamina	24·9 ± 0·4*		–	N/A
	Trap	20·8 ± 0·9*			
Drosera capensis (Pavlovič *et al*., 2014)	Trap		0·93 ± 0·10 (0·74 ± 0·38)	N/A	0
Drosera prolifera (Adamec, 2010*a*)	Lamina	7·16 ± 0·70*		+†	N/A
	Tentacles	52·0 ± 7·5*			
Nepenthes alata (Pavlovič *et al*., 2007)	Lamina	9·7 ± 0·9		–	N/A
	Trap	6·3 ± 1·1			
Nepenthes alata (He and Zain, 2012)	Lamina		Approx. 2‡	–	N/A
	Trap		Approx. 1‡		
Nepenthes ampullaria (Pavlovič *et al*., 2011*b*)	Lamina		0·54 ± 0·10 (0·59 ± 0·05)	–	0
	Trap		0·35 ± 0·06 (0·38 ± 0·06)		
Nepenthes mirabilis (Pavlovič *et al*., 2007)	Lamina	8·0 ± 0·6		0	N/A
	Trap	11·6 ± 0·9			
Nepenthes talangensis (Pavlovič *et al*., 2009)	Lamina	5·8 ± 0·5 (7·0 ± 0·21)	0·97 ± 0·02 (1·15 ± 0·06)	0/– (g^{-1} d. wt/m^{-2})	0
	Trap	6·5 ± 0·4 (9·6 ± 1·7)	0·43 ± 0·02 (0·60 ± 0·10)		
Nepenthes ventricosa (Adamec, 2010*a*)	Lamina	5·86 ± 0·93*		0	N/A
	Trap	8·20 ± 1·47*			
Pinguicula vulgaris (Méndez and Karlsson, 1999)	Plant	19·2 ± 8·1 (s.d.) (23·1 ± 8·2) (s.d.)	0·8 ± 0·3 (s.d.) (1·0 ± 0·4) (s.d.)	N/A	0
Sarracenia minor (Adamec, 2010*a*)	Wing	4·79 ± 0·27*		–	N/A
	Trap	3·76 ± 0·25*			
Sarracenia psittacina (Adamec, 2010*a*)	Wing	2·28 ± 0·25*		0	N/A
	Trap	2·40 ± 0·49*			
Sarracenia purpurea (Adamec, 2010*a*)	Wing	5·81 ± 0·62*		+	N/A
	Trap	8·38 ± 0·32*			
Sarracenia purpurea (Hájek and Adamec, 2010)	Wing	9·5 ± 1·1		N/A	N/A
	Trap	12·6 ± 0·9			
Sarracenia rubra (Adamec, 2010*a*)	Wing	5·57 ± 0·20*		0	N/A
	Trap	4·98 ± 0·41*			
Utricularia australis (aq) (Adamec, 2008)	Leaf	7·89 ± 0·68 (7·42 ± 0·93)		N/A	0
Utricularia australis (aq) (Adamec, 2006)	Leaf	4·86 ± 0·23		+†	N/A
	Trap	8·56 ± 0·35			
Utricularia bremii (aq) (Adamec, 2006)	Leaf	3·07 ± 0·36		+†	N/A
	Trap	7·02 ± 0·45			
Utricularia floridana (aq) (Adamec, 2006)	Leaf	2·65 ± 0·29		+†	N/A
	Trap	5·09 ± 0·33			
Utricularia intermedia (aq) (Adamec, 2006)	Leaf	3·48 ± 0·34		+†	N/A
	Trap	6·77 ± 0·57			
Utricularia macrorhiza (aq) (Knight, 1992)	Leaf	0·751§		0	N/A
	Trap	0·804§			
Utricularia ochroleuca (aq) (Adamec, 2006)	Leaf	1·73 ± 0·17		+†	N/A
	Trap	5·15 ± 0·42			
Utricularia vulgaris (aq) (Adamec, 2006)	Leaf	3·94 ± 0·36		+†	N/A
	Trap	7·49 ± 0·21			
Summary				(+) 9†	(+) 0
				(–) 7	(–) 0
				(0) 9	(0) 7

A positive response is indicated by '+', a negative response by '–', no response by '0', no data by 'N/A'.
Note the different unit for aquatic carnivorous plants (R_{Daq}).
Means ± s.e. whenever possible (or s.d. if indicated).
*Values are in nmol O_2 g^{-1} d. wt s^{-1}.
†Active trap (electrical signalling or water pumping).
‡Values are in μmol O_2 m^{-2} s^{-1}.
§Values are in mg C g $tissue^{-1}$ h^{-1} from a population in Grassy Lake.

As a result of our analysis, it is evident that the energetic or respiration costs of traps in comparison with leaves greatly depend on the type of the trap, whether it is active or passive (Table 2). In passive pitcher traps of *Sarracenia*, *Cephalotus* and *Nepenthes*, the difference in R_D between traps and leaves (or pitcher walls and wings) is rather small or ambiguous. In many cases (seven out of 24 cases in Table 2), the R_D in the passive traps is even lower than in the leaves, probably as a consequence of reduced A_N or due to a different leaf mass area (LMA) of these two distinct organs and not to specialization for carnivory, as is documented in the case of *N. talangensis* (Pavlovič *et al*., 2007, 2009; Adamec, 2010*a*, Hájek and Adamec, 2010; Table 2). Because the R_D in traps is comparable with that in leaves (Table 2) and traps have lower A_N than leaves (Table 1), traps and carnivorous plants have a higher R_D/A_N ratio (Bruzzese *et al*., 2010; Hájek and Adamec, 2010). In the active but resting traps of *Dionaea* and *Drosera* differences in R_D between the trap and petiole are also negligible (Adamec, 2010*a*; Hájek and Adamec, 2010; Table 2). However during their action, spatio-temporal changes in A_N and R_D occur. Pavlovič *et al*. (2010*a*) showed that A_N and ϕ_{PSII} decreased and R_D increased in response to trigger hair stimulation, simulating prey capture and retention in *Dionaea muscipula*. As a result of decreased photochemistry, non-photochemical quenching dissipates the absorbed light energy safely (Fig. 4A–C). Jaffe (1973) and Williams and Bennett (1982) showed that traps of *Dionaea* are expensive, and during trap closure about 29 % of the cellular ATP is lost; this is used for rapid transport of water, resulting in changes in turgor pressure and subsequent closure of the trap. Pavlovič *et al*. (2010*a*) showed that rapid changes of A_N and R_D in the Venus flytrap are due to trigger hair stimulation which generates electrical signals (action potentials, APs) and is independent of trap closure: 'single hair irritation' and the 'prey struggle phase in the closed trap' also resulted in reduction of A_N and stimulation of R_D (Fig. 4A–D). Volkov *et al*. (2007, 2008) and Pavlovič and Mancuso (2011) found that action potential signalling and changes in R_D and A_N in *Dionaea* are confined to the traps and are not propagated to the photosynthetic laminae, what may decrease the overall costs. In their subsequent studies, they found that mainly dark enzymatic reactions are targeted, with a negligible effect on light reactions of photosynthesis (Pavlovič *et al*., 2011*a*; Vredenberg and Pavlovič, 2013). The effect of electrical signals on photosynthesis and respiration in plants is now well recognized (for reviews, see Fromm and Lautner, 2007; Pavlovič, 2012*b*; Gallé *et al*., 2015). Increased R_D was also found in separated tentacles of *Drosera prolifera* in the study of Adamec (2010*a*), and the author suggested that such an increase is also probably due to electrical signalling in tentacles (Williams and Pickard, 1972*a*, *b*; Table 2). Because consumption of ATP during action potentials was documented (Beilby, 2007), the decrease in the ATP/ADP ratio after APs seems to be the factor increasing R_D (Pavlovič *et al*., 2011*a*). It is very likely that a similar response of APs on photosynthesis and respiration also occurs in the aquatic carnivorous plant *Aldrovanda vesiculosa*; however this plant has never been studied in this respect.

The high metabolic or energetic costs of traps also occur during prey digestion. Kruse *et al*. (2014) found increased R_D during the digestive period of the Venus flytrap, hence resulting in a significantly greater R_D/A_N ratio. We measured the light response curve of photosynthesis and we also found higher R_D 36 h after induction of digestion (Fig. 4E, at zero irradiance). This is in accordance with the observations of Robins and Juniper (1980), who found that the mitochondria of stimulated *D. muscipula* glands closely resemble mitochondria of active animal tissue. Following stimulation, the mitochondria become extended, greatly increasing their surface to volume ratio accompanied by an increase in the density of cristae. Recently, Gao *et al*. (2015) found that fed *D. muscipula* traps are frequently short of organic carbon (probably spent by R_D and enzyme production), so that they even attract carbon resources from the roots. The behaviour of glands in passive pitcher traps has never been investigated in this respect, so we cannot exclude the possibility that they also increase R_D in response to prey capture.

Besides digestion, some chemicals in insect prey can also affect carbon metabolism in carnivorous plants. Using chlorophyll fluorescence imaging, Pavlovič (2010) found that formic acid in ants, a common prey of carnivorous plants, strongly inhibits the photosynthetic reaction in PSII during digestion in *Drosera capensis*. Formic acid inhibits electron transport on the acceptor side of PSII, particularly from plastoquinone A to plastoquinone B.

What is the benefit of costly electrical signalling in carnivorous plants? For a successful hunt, the fast trap closure triggered by electrical signals must be faster than the prey escape reaction. Electrical signalling is carbon costly in term of decreased A_N and increased R_D; however, successful insect capture and digestion provides a significant amount of nutrients which can later stimulate photosynthesis (Pavlovič *et al*., 2010; Kruse *et al*., 2014). However, the importance of cost–benefit analysis of electrical signalling in carnivorous plants goes beyond fast prey capture. After the rapid closure secures the prey, repeated mechanical stimulation of trigger hairs by struggling prey and generation of hundreds of APs result in further closure and tightening of the trap to a tightly appressed state and secretion of digestive fluid (Affolter and Olivo, 1975). Escalante-Peréz *et al*. (2011) found that 30 min after prey capture in the Venus flytrap, the level of the jasmonic acid (JA) precursor, 12-oxophytodienoic acid (OPDA), increased. Libiaková *et al*. (2014) also found in the same species an increased level of jasmonates in response to mechanical and chemical stimuli (Fig. 4F). Nakamura *et al*. (2013) and Mithöfer *et al*. (2014) found an increased level of JA and its bioactive isoleucine conjugate (JA-Ile) in *Drosera capensis* in response to prey capture. Libiaková *et al*. (2014) suggested that jasmonate molecules can regulate production of digestive enzymes in response to mechanical and chemical stimuli from prey. It has been found that mechanical and subsequent electrical activity is not sufficient to trigger the full enzymatic capacity in *Drosera* and *Dionaea*, and some chemical signals must be involved (Matušíková *et al*., 2005; Libiaková *et al*., 2014; Pavlovič *et al*., 2014). External application of JA or coronatine, a structural mimic of JA-Ile, bypasses mechanical and chemical signalling and initiates secretion of digestive fluid with high proteolytic activity of the cysteine endopeptidase Dionain, and induces transcription of type I chitinase and ammonium channels in the Venus flytrap (Escalante-Pérez *et al*., 2011; Scherzer *et al*., 2013; Paszota *et al*., 2014; Libiaková *et al*., 2014). The link between electrical and jasmonate signalling is not novel and has been documented

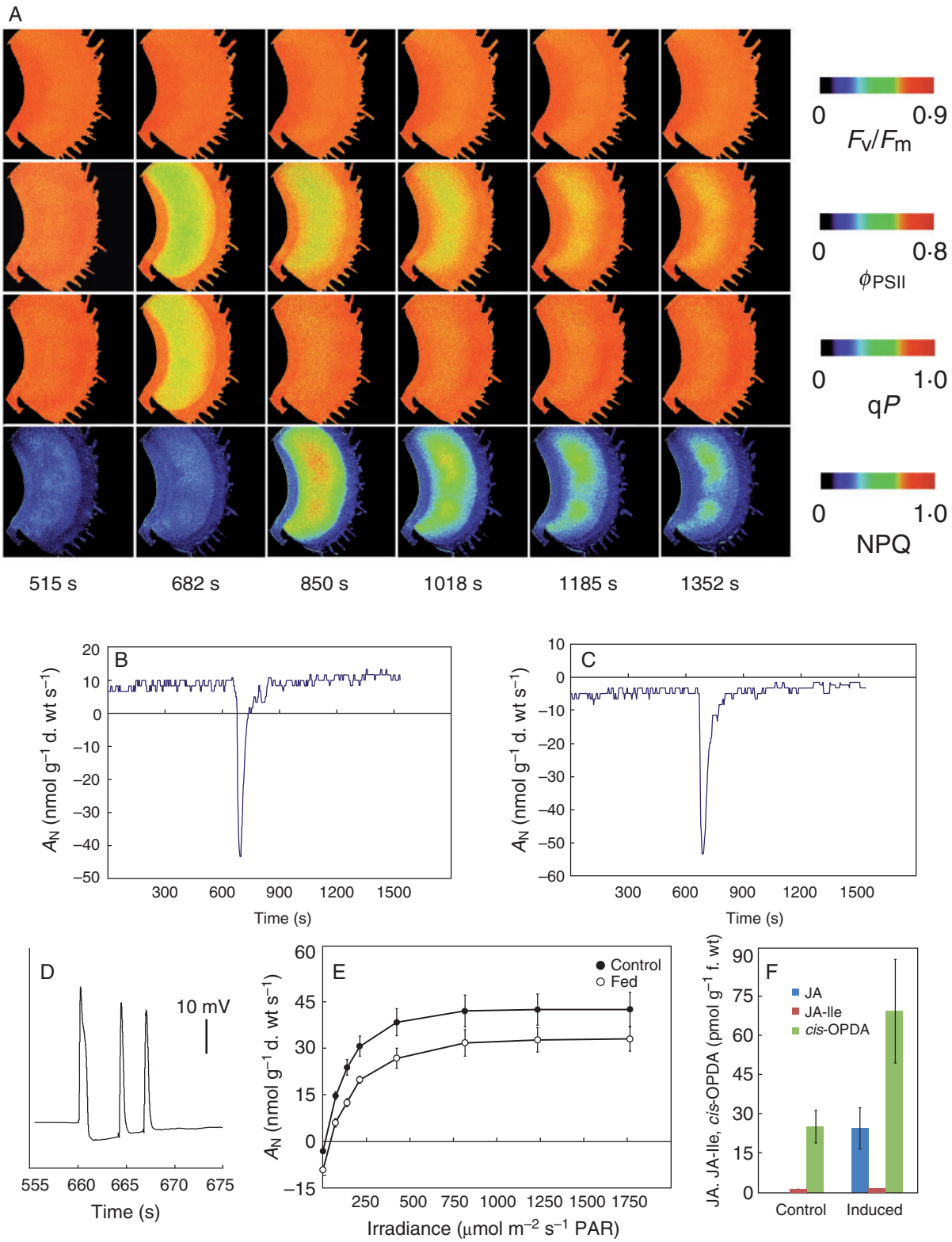

FIG. 4. A novel insight into the cost–benefit model in the Venus flytrap (*Dionaea muscipula*). (A) Spatio-temporal changes of chlorophyll *a* fluorescence in response to mechanical touches of trigger hairs (at time 660–670 s) and generation of action potentials, maximum quantum yield of photosystem II (F_v/F_m), effective photochemical quantum yield of photosystem II (ϕ_{PSII}), photochemical quenching (q*P*) and non-photochemical quenching (NPQ); for detailed explanations of the kinetics of chlorophyll *a* fluorescence in Venus flytrap see Pavlovič *et al.* (2011*a*). (B) Simultaneous measurement of gas exchange at a light intensity of 80 μmol m^{-2} s^{-1} PAR. (C) Measurement of gas exchange in the dark indicating the rate of respiration (R_D). (D) Action potentials in the trap in response to mechanical stimulation of trigger hairs. (E) Light response curve of photosynthesis in open control traps and traps in the digestive period 36 h after chemical stimulation with NH_4Cl. (D) The endogenous jasmonate level (JA, jasmonic acid; JA-Ile, isoleucine conjugate of jasmonic acid; *cis*-OPDA, *cis*-12-oxophytodienoic acid) in trap tissue 36 h after induction with NH_4Cl. Data are means ± s.e. ($n = 5$). For details of the methods, see the Supplementary Data.

in the systemic response in many non-carnivorous plants (e.g. Hlaváčková *et al*., 2006; Mousavi *et al*., 2013). Jasmonates are lipid-derived compounds acting as key signalling molecules in plant stress and defence responses (Wasternack and Hause, 2013), and their accumulation is probably dependent on a cytosolic Ca^{2+} increase (Fisahn *et al*., 2004; Vadassery *et al*., 2014). In the sites that receive the electrical signals, jasmonates mediate defence-responsive gene expression (Mousavi *et al*., 2013). These induced defences are generally believed to have evolved as a resource-saving strategy because JA acts as a signal to redirect the gene expression and biosynthetic capacity from photosynthesis and growth to defence, and that represent a significant allocation cost for plants, which might be offset by the fitness benefit of not incurring these costs, when defence is not needed (Heil and Baldwin, 2002; Meldau *et al*., 2012; Vos *et al*., 2013; Attaran *et al*., 2014). Moreover, jasmonates inhibit photosynthetic reactions and repress transcription of many photosynthesis-related genes (Herde *et al*., 1997; Heil and Baldwin, 2002; Hlaváčková *et al*., 2006; Nabity *et al*., 2013; Attaran *et al*., 2014). This cost–benefit explanation has been widely applied to evolution and maintenance of inducible defence (Baldwin, 1998; Heil and Baldwin, 2002; Vos *et al*., 2013). The finding that jasmonates play a role in plant carnivory is not surprising, because it is now believed that carnivory has evolved from plant defence mechanisms (Juniper *et al*., 1989; Hatano and Hamada, 2012). The possible hierarchy of consecutive events in trap tissue which are initiated by prey capture adopted from plant defence mechanisms is suggested in Fig. 5. Thus electrical and jasmonate signalling is beneficial for regulation of enzyme and transporter expression in carnivorous plants with active trapping mechanisms, and inducibility allows carnivorous plants to forgo the allocation costs when the prey in the trap is not present. In Fig. 4E, F, the increased accumulation of jasmonates in Venus flytraps 36 h after induction of digestion and decreased A_N can be seen. Whether the reduction of A_N is the result of increased R_D (as discussed above) or reduced photosynthesis as a result of allocation costs is unclear. Venus flytraps strongly change their trap shape from the open to narrowed phase, which complicates interpretation of the data due to the changes of light interception. Nevertheless, an increased R_D/A_N ratio is an indicator of substantial cost during the digestive period in the Venus flytrap (Kruse *et al*., 2014). These costs are, however, offset by the benefits of not incurring these costs when digestion is not needed. It remains to be elucidated whether the jasmonates accumulate only in digestive glands or also in mesophyll tissue, and where exactly they reprogramme the gene expression.

This may seem to be in contrast to pitcher plants, which are considered to have passive traps (Juniper *et al*., 1989). In contrast to Venus flytraps, the digestive fluid and enzymes in carnivorous plants of the genus *Nepenthes* are present even in the pitcher traps without captured prey (Eilenberg *et al*., 2006; Hatano and Hamada 2008, 2012). Indeed, some of the digestive enzymes are constitutively expressed (type I chitinase *Nkchit2b* and S-like RNAase *cf-I* in *Nepenthes khasiana* and *Cephalotus follicularis*, respectively; Eilenberg *et al*., 2006; Nishimura *et al*., 2013). However, transcription of some carnivory-related genes in the genus *Nepenthes* is also regulated by the presence of prey, such as ammonium transporter *NaAMT1*, H^+-ATPase *NaPHA3*, type I chitinase *Nkchit1b*, type III chitinase *Nrchit1* and thaumatin-like protein (Schulze *et al*., 1999; An *et al*., 2001; Eilenberg *et al*., 2006; Rottloff *et al*., 2011, 2013). Hatano and Hamada (2012) identified new proteins in digestive fluid of *N. alata* in response to chitin addition: class III peroxidase (NaPrx1a), β-1,3-glucanase (NaBGLUC2) and class III chitinase (NaCHIT3). Expression of protease, RNase, nuclease and phosphatase is also induced by the presence of appropriate chemical signals (such as nucleic acids, protein and reduced N) in the passive trap of *Sarracenia purpurea* (Gallie and Chang, 1997). Although the electrical signals have never been documented in passive pitcher traps, the intracellular measurements of membrane potential in the glands of Venus flytrap showed that application of NH_4^+, the most effective inductor in carnivorous plants, resulted in strong depolarization of membrane potentials due to the action of the ammonium transporter DmAMT1 and even triggered APs (Scherzer *et al*., 2013). A similar ammonium transporter NaAMT1 was immunodetected in the glands of the carnivorous plant *Nepenthes alata* (Schulze *et al*., 1999), and NH_4^+ is rapidly taken up from digestive fluid (An *et al*., 2001; Moran *et al*., 2010); however, no electrophysiological measurements have been done in this species. Also what kind of molecule or phytohormone is involved in transduction of stimuli from prey to changes of gene expression is unknown. It is tempting to assume that carnivorous pitcher traps are not so passive and electrically silent as was previously believed and more investigation in this genus is needed. In contrast, very active traps of bladderworts (*Utricularia* sp.) probably have constitutive enzyme production and besides enzymes also rely on microbial digestion (Sirová *et al*., 2003, 2010, 2011; Adamec *et al*., 2011).

ARE ALL CARNIVOROUS PLANTS REALLY CARNIVOROUS?

Our perception of carnivorous plants as merciless killers catching anything that is moving and careless is being changed. As the first, Cresswell (1998) reported that over half of the weight of dead matter found in the pitchers of *Nepenthes ampullaria* in Borneo was plant derived. This observation was supported by a study of Moran *et al*. (2003) who proposed that *N. ampullaria* exhibits a leaf litter trapping syndrome. The leaf litter trapping syndrome in plants is not novel and is very common in non-carnivorous tank epiphytic bromeliads (Givnish *et al*., 1997, 2014; Dézerald *et al*., 2013). The *N. ampullaria* plant has adapted to this alternative nutrition by an unusual growth pattern and pitcher morphology:

1. the pitcher lid is reflexed away from pitcher mouth and allows debris to fall directly into the pitcher;
2. the pitchers sit above the soil surface in a tightly packed 'carpet' and the upper pitchers are only rarely produced on the climbing stem;
3. *Nepenthes ampullaria* is often found growing beneath the forest canopy, whereas most other lowland species are found predominantly in open, secondary vegetation.

The 'rain' of debris from the canopy and tightly packed 'carpet' of pitchers positioned above the soil surface may intercept this source of nutrient before it reaches roots of other non-carnivorous species and may provide competitive advantage

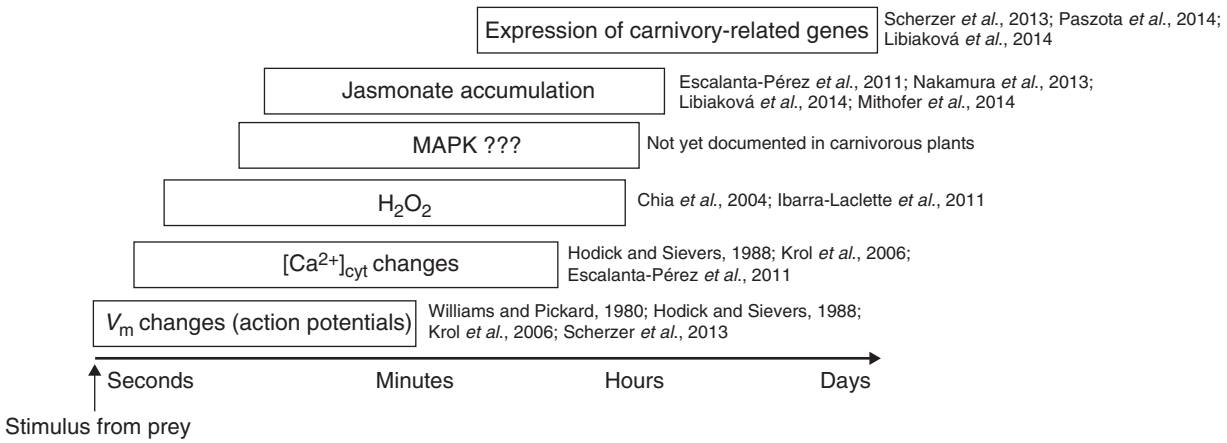

FIG. 5. Probable timed hierarchy of consecutive events detectable in carnivorous plants with the active trapping mechanism in response to prey capture adopted from plant defence mechanisms (Maffei *et al.*, 2007). The earliest events measurable are action potentials generated by mechanical stimuli (Williams and Pickard, 1980; Hodick and Sievers, 1988; Krol *et al.*, 2006; Escalante-Pérez *et al.*, 2011) or chemical stimuli from prey (Scherzer *et al.*, 2013), which trigger a cytosolic calcium increase (Escalante-Pérez *et al.*, 2011) and generation of H_2O_2 (Chia *et al.*, 2004; Ibarra-Laclette *et al.*, 2011). Increased cytosolic Ca^{2+} is probably sensed by binding to calmodulin protein (CaM) or other calcium-sensing proteins, which can interact with mitogen-activated protein kinases (MAPKs; this part of the signaling pathway has not yet been documented in carnivorous plants). MAPKs regulate biosynthesis of jasmonates which trigger the expression of carnivory-related genes (Scherzer *et al.*, 2013; Nakamura *et al.*, 2013; Libiaková *et al.*, 2014; Mithöfer *et al.*, 2014; Paszota *et al.*, 2014).

over non-carnivorous plants co-occurring in the same habitat (Fig. 6A). On the other hand, some traits involved in prey attraction (nectar glands) and retention (waxy zone and lunate cells) are reduced or absent and some are still present (large slippery peristome, chitinase in digestive fluid) (Clarke and Moran 2001; Moran *et al.* 2003; Rottloff *et al.*, 2011).

Other species, such as *Nepenthes lowii*, produce pitchers lacking the features normally associated with arthropod prey capture – slippery peristome, waxy zone and viscoelastic digestive fluid. This species is perhaps the most unusual in the genus, being characterized by its strongly constricted upper pitchers with a reflexed lid and numerous bristles on its lower surface (Fig. 6B). Clarke *et al.* (1997) found that the aerial pitcher of *N. lowii* contained large amounts of vertebrate faeces, but no invertebrate prey. This combination of aerial pitcher characteristics and contents indicated a possible interaction with vertebrates. Clarke *et al.* (2009) resolved the special adaptation of this species definitively when they filmed the tree shrew *Tupaia montana* defecating into the pitchers after feeding on exudates that accumulate on the pitcher lid. Stable N isotope analysis revealed that tree shrew faeces account for between 57 and 100 % of foliar N in mature *N. lowii* plants. This unique nutrient sequestration strategy was later also found in two other species of the genus (*N. rajah* and *N. macrophylla*; Chin *et al.*, 2010). On the basis of unique morphological characteristics of all three species, Chin *et al.* (2010) concluded that extraordinary modifications to nutrient acquisition strategies in carnivorous plants may occur through simple modifications of trap geometry. The pitchers of *N. lowii*, *N. rajah* and *N. macrophylla* with large orifices, and lids that are concave, elongated and oriented approximately at right angles to the orifice capture faeces of the tree shrew *T. montana*, whose body size is optimal to defecate into the pitchers (Fig. 6C). Moreover, all three *Nepenthes* species were shown to produce visual signals, in which the underside of the pitcher lid stood out in high contrast to the adjacent area on the pitcher, in the blue and green wavebands visible to the tree shrews (Moran *et al.*, 2012). Analysis of volatiles extracted from the secretions of the pitcher lids by gas chromatography coupled to mass spectrometry (GC/MS) revealed 44 volatile compounds, including hydrocarbons, alcohols, esters, ketones and sulphur-containing compounds, which are commonly present in sweet fruit and flower odours (Wells *et al.*, 2011). The body of a drowned tree shrew is occasionally found in the pitcher of *N. rajah*, providing much greater benefits than droppings. Recently it has been documented that beside diurnal *T. montana*, the nocturnal summit rat (*Rattus baluensis*) also defecates into the *N. rajah* pitchers. Temporal segregation of pitcher visits by the two mammal species enables *T. montana* and *R. baluensis* to exploit the same resource whilst largely avoiding direct conflict (Greenwood *et al.*, 2011; Wells *et al.*, 2011).

The pitchers of *Nepenthes rafflesiana* var. *elongata* (recently described as the new taxon *Nepenthes hemsleyana*; Scharmann and Grafe, 2013) is very similar to the typical form of *N. rafflesiana*, but is elongated in all respects. Hardwicke's woolly bats (*Kerivoula hardwickii*) roost in the upper pitchers of *N. hemsleyana*. The elongated pitchers provide enough space for the bats and in return the plant receives additional N input in the form of faeces. It has been estimated that the plant derives 33·8 % of its total foliar N from the bat's droppings; however, only 20·8 % of traps are occupied (Grafe *et al.*, 2011).

The fact that the genus *Nepenthes* demonstrates a remarkable variety in pitcher morphology implies that it may be a candidate model for adaptive radiation with regard to N sequestration strategies (Chin *et al.*, 2010; Pavlovič, 2012*a*). If the changes in pitcher morphology are adaptive, the plant will obtain some increment in fitness. Pavlovič *et al.* (2011*b*) tested the hypothesis of whether leaf litter utilization by *N. ampullaria* can increase photosynthetic efficiency according to Givnish's cost–benefit model. They found that leaf litter utilization slightly increased A_N; however, the nutrient stress was not completely alleviated in comparison with experiments with insect prey (Pavlovič *et al.*, 2009). It seems that these unique nutrient sequestration strategies make the best of a bad situation.

Fig. 6. Unique nutrient sequestration strategies in three species of *Nepenthes* from Borneo. (A) Leaf litter utilization by *N. ampullaria*. (B) Pitcher plants *N. lowii* and *N. rajah* (C) have modified pitcher morphology for collecting faeces from the mountain tree shrew (*Tupaia montana*).

Because the insect body contains around 9·8 % (Pavlovič *et al.*, 2009), animal faeces 4·9 % (Chin *et al.*, 2010) and the leaves of co-habiting plant species only 1·2 % of N (Osunkoya *et al.*, 2007), the animal prey is still the best source of N. This might explain why the plants do not completely rely on alternative sources of nutrients and still capture some insect prey (Pavlovič *et al.*, 2011*b*).

A unique sequestration strategy is not confined to *Nepenthes*. *Roridula* plants capture insects by using a sticky hydrophobic secretion on the heads of immobile tentacles. It has been hypothesized that *Roridula* leaves absorb N from the faeces of the obligately associated, carnivorous hemipteran bug *Pameridea roridulae* (Anderson, 2005; Plachno *et al.*, 2009). Also, the non-carnivorous plants *Bromelia balansae* and *Paepalanthus bromelioides* (now considered as carnivorous) obtain a significant amount of N from spider faeces (Romero *et al.*, 2006; Nishi *et al.*, 2013) as does *Vriesea gigantea* from amphibian excrement (Inselsbacher *et al.*, 2007). Peroutka *et al.* (2008) documented that algae of 45 genera were found in *Utricularia* bladders, which form up to 80 % of total prey. Ninety per cent of them were dead. This is the reason why the authors named their paper appropriately: '*Utricularia* – a vegetarian

carnivorous plant'. The algae probably entered the traps due to an incidental and spontaneous firing (Adamec, 2011, 2012; Vincent *et al*., 2011*a*). Koller-Peroutka *et al*. (2015) confirmed the ecological importance of autonomous firing in *Utricularia* and found that the contribution of pollen grains and algae to the nutrition of *Utricularia* plant is comparable with the benefit gained from prey animals. Harder and Zemlin (1968) demonstrated in axenic cultures of *Pinguicula lusitanica*, grown on agar without N and P for 8 weeks, nutrient utilization from supplied *Pinus* pollen. The pollen-fed plants grew faster, contained more chlorophyll, and aged more slowly. In contrast to unfed plants, they initiated flower buds very early and flowered richly. Thus, the *Pinguicula* species with broad leaves (and possibly also some *Drosera*, e.g. *Drosera schizandra* growing beneath the forest canopy in Queensland) may benefit from aerial rain of pollen and probably also of spores, seeds and leaf fragments under natural conditions.

CONCLUSIONS

In 2014 the cost–benefit model for evolution of plant carnivory celebrated 30 years of existence. During that time, the cost–benefit model became a framework for interpretation of results from a wide range of experimental studies on many carnivorous plant species. The relationship between nutrients gained from prey digestion and photosynthesis has been central in cost–benefit model analyses. In the years since the cost–benefit model was initially proposed, several studies have now confirmed two of its key assumptions, showing both that traps have lower photosynthetic rates than asimilatory leaves, and that photosynthesis of carnivorous plants increases as a result of feeding (Table 1). Recent research has shown that active trapping mechanisms are costly in terms of spatial and temporal activation of respiration and inactivation of photosynthesis. Water pumping in *Utricularia* bladders, prey digestion, and electrical signalling in *Dionaea*, *Drosera* and probably *Aldrovanda* represent energetic costs for plants. Against these, jasmonate signalling has evolved as a cost-saving strategy, because instead of producing costly digestive enzymes permanently, carnivorous plants often activate their production only in response to electrical and chemical signals that implicate the presence of prey. The involvement of jasmonates and chitinases in the digestive process support the hypothesis that carnivory may have evolved from plant defence mechanisms – and it is not only the carnivory. Recent works have revealed different strategies that carnivorous plants employ in acquiring nutrients and that the cost–benefit model can also be applied here.

SUPPLEMENTARY DATA

Supplementary data are available online at www.aob.oxfordjournals.org and give the materials and methods for the data in Figs 3 and 4.

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