Commentary

Shedding light on photosynthesis in carnivorous plants. A commentary on: '*Nepenthes* × *ventrata* photosynthesis under different nutrient applications'

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Carnivorous plants have inspired generations of scientists. About 800 species have evolved various forms of leaf-derived trap that attract, capture, retain, kill and digest animal prey, as a mode of survival in nutrient-poor environments. Since Charles Darwin provided the first evidence for carnivory in plants, the benefits of this life history mode have been well documented, including the enhancement of photosynthetic efficiency in response to nutrient uptake from prey. Givnish *et al.* (1984) presented a compelling cost–benefit model predicting that carnivory is an evolutionarily stable strategy in habitats where nutrients – in particular N – are limiting, but light and water are plentiful (Fig. 1A,D). According to the model (Fig. 1D), prey-derived N should boost the production of chlorophyll and Rubisco, thereby enhancing photosynthetic assimilation rates. While the photosynthesis-enhancing effects of prey intake are well documented and appear to be consistent across carnivorous lineages (Pavlovič and Saganová, 2015), the underlying physiological mechanisms remain poorly understood. In this issue of *Annals of Botany*, Capó-Baucà *et al.* (2020) present the most comprehensive investigation of how prey capture affects the photosynthetic apparatus in a carnivorous pitcher plant to date.

The genus *Nepenthes* (Fig. 1A,B), which is the focus of the current study, is the most species-rich of the three major (unrelated) lineages of carnivorous pitcher plants, and is distributed predominantly in the Malay Archipelago. Despite growing interest in the genus as models for evolutionary research (Whitewoods *et al.*, 2020) and natural blueprints for bioinspired technologies (Bushan, 2009), surprisingly few studies have addressed fundamental questions on the physiology of carnivorous plants. The few that have indicate that a complex interplay exists between nutrient quantity, source and mode of uptake on the one hand, and nutrient allocation and growth rate, photosynthetic efficiency, and reproductive success on the other (Fig. 1C) (Adamec and Pavlovič, 2018). Together, this body of work suggests a fundamental trade-off: leaves are modified into traps at the expense of photosynthetic efficiency because traits that make an effective insect trap are different from, and largely incompatible with, those that make an efficient light trap. As a result, traps contribute little to the, already comparatively low, photosynthetic performance of carnivorous plants (Fig. 1B). In pitcher plants this conundrum is solved either by spatial separation (insect and light-trapping functions in different parts of the leaf) or by temporal separation (the production of two distinct leaf types). A remarkable developmental plasticity enables pitcher plants to respond to nutrient availability by reallocating investment to photosynthetically active (non-carnivorous) parts of the plant when sufficient N is available (Ellison and Farnsworth, 2008). When N is limiting, investment is shifted towards the production of traps, thereby investing in enhanced nutrient acquisition through carnivory. Several studies have shown that the N-content of pitchers is significantly lower than that of photosynthetic organs
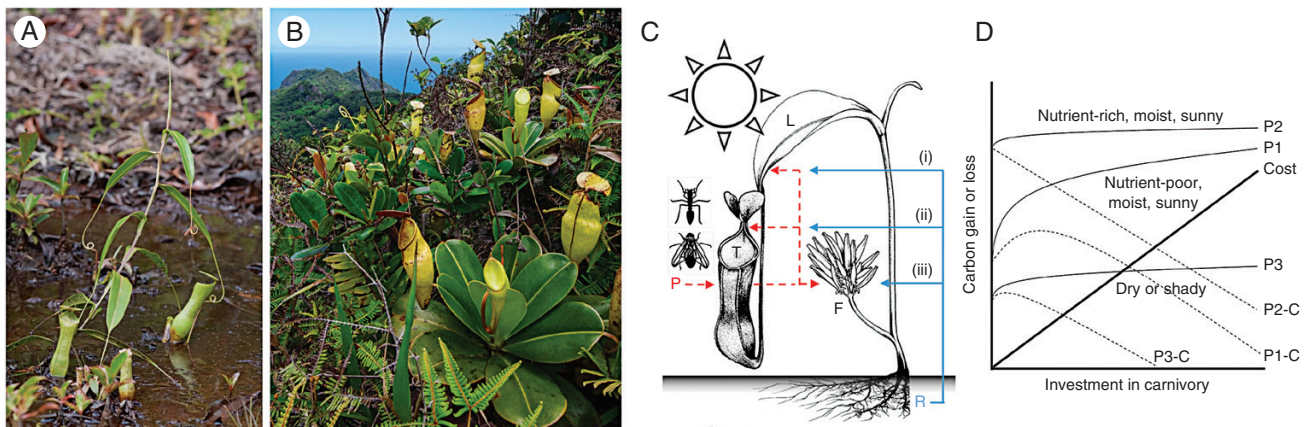

FIG. 1. (A) *Nepenthes gracilis* pitcher plant growing in a typical sunny, wet, nutrient-poor habitat in northern Borneo. (B) *Nepenthes pervillei* showing green, chlorophyll-rich leaf laminae and yellow, chlorophyll-poor traps. (C) The complex interplay between the investment of soil-borne nutrients (blue line) from the roots (R), and prey-borne nutrients (red broken line) from the trap (T) into either (i) photosynthesis, especially by the photosynthetically efficient leaf lamina (L), (ii) trapping efficiency (of different forms of prey, P) by the photosynthetically inefficient pitcher trap and (iii) to the flowers/fruits (F), i.e. the plant's reproductive potential. (C) A simplified cost–benefit model for carnivory showing the rate of increase in photosynthesis (P) under different conditions (1–3). Grey broken lines represent the net difference between photosynthetic benefit and cost (C) of obtaining nutrients by carnivory. The greatest rate (1) is in nutrient-poor, moist, sunny environments where the benefit of a small investment in carnivory exceeds its own cost. Adapted from Givnish *et al.* (2018).

(Ellison and Farnsworth, 2008; Osunkoya *et al.*, 2008), and that this is at least partly due to the low Rubisco content of pitchers (Pavlovič and Saganová, 2015).

Together, this recent research corroborates the predictions of Givnish's cost–benefit model, although the underlying physiological mechanisms remain elusive. In particular, it remains unclear what limits photosynthesis (and hence growth) in carnivorous plants: stomatal conductance, internal transport processes or the biochemical efficiency of the photosystems? In this issue, Capó-Bauçà *et al.* help to close this knowledge gap by quantifying photosynthesis in response to nutrient application, whether that is by adding insect prey to traps or mineral nutrients via the roots. In contrast to previous studies, they measure not only a suite of key photosynthesis parameters – gas exchange, chlorophyll fluorescence and photosynthesis-related leaf proteins together with the mineral composition and N and C isotopic discrimination of both leaves and prey insects – but also the effects of supplying four different types of prey, representative of the natural prey spectrum of the plants.

Capó-Bauçà *et al.* show for the first time that photosynthesis in nutrient-stressed *N.* × *ventrata* is limited by parenchymatic CO_2 diffusion rather than by intrinsic biochemical efficiency. Remarkably, this limitation is lifted when sufficient nutrients are supplied, and biochemistry becomes the new limiting factor. The addition of nutrients from prey or mineral sources led to a general accumulation of leaf protein complexes involved in the photochemical assimilation process: chlorophyll, chlorophyll-binding proteins, components of the oxygen evolving complex and electron transport chain, as well as ATPase and Rubisco. The increase in photosynthetic rate was matched by enhanced growth rates after nutrient addition. In line with previous studies, Capó-Bauçà *et al.* observed a shift in biomass investment towards photosynthetic leaves (and away from traps) in root-fertilized treatments. Interestingly, they observed differences in N bioavailability among the four different types of insects fed to the pitchers, highlighting the importance of examining a range of prey species. Significantly, it remains unclear whether the observed difference in biomass allocation

to vegetative organs was due to the nature of the nutrient source (insects or inorganic solution), or to the mode of administration (via the roots rather than the pitchers). An additional treatment with mineral fertilizer applied to the pitchers would address this question. As Capó-Bauçà *et al.* assert, the investment in carnivory is likely to be controlled by both the quantity and the form of nutrient input, highlighting the importance of robust experimental design when examining the effects of carnivory on plant physiology.

The last two decades have seen a step change in our understanding of the physiology of carnivorous plants in relation to nutrient acquisition. Capó-Bauçà *et al.* shed further light on the functional consequences of plant carnivory, which have received significantly less scientific attention than, for example, the mechanisms of prey capture and digestion. Laboratory experiments using commercial cultivars cannot capture the diversity of interactions in natural systems, for example among microclimate, prey diversity and pitcher-inhabiting microfauna. Nevertheless, the present study does provide new insights into the benefits of carnivory that form a key assumption of Givnish's cost–benefit model. Future studies should attempt to study the interplay of nutrient intake and allocation on the one hand, and photosynthesis and growth on the other, in natural habitats. Furthermore, we need to explore how the physiological limitations identified by Capó-Bauçà *et al.* apply to other carnivorous plants such as sundews, Venus flytraps and bladderworts. Both construction and maintenance costs of traps vary considerably among species (Osunkoya *et al.*, 2008; Pavlovič and Saganová, 2015), and photosynthesis in aquatic bladderworts is likely to be limited by CO_2 availability rather than by nutrient supply (Adamec, 2008). When further species are added to the picture, along with data on their prey and nutrient assimilation in natural systems, the needle will move once again on our understanding of the effects of carnivory on plant physiology.

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