Functional Ecology

British Ecological Society

Functional Ecology 2008, **22**, 728–737 doi: 10.1111/j.1365-2435.2008.01421.x

Modelling the relationship between a pitcher plant (*Sarracenia purpurea*) and its phytotelma community: mutualism or parasitism?

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Summary

1. To improve our understanding of the relationship between the pitcher plant (*Sarracenia purpurea*) and the phytotelma community inhabiting its leaves we built an exploratory, mechanistic model based on stochiometric constraints on carbon and nitrogen associated with prey decomposition.

2. Our theoretical results suggest that the phytotelma community is acting as a mineralizing system producing nitrogen for the plant. This is confirmed by data collected in the field and in the literature, that show the amount of nitrogen produced by the decomposition of prey is sufficiently high to be considered as a major source of nitrogen for the plant.

3. In our model, nitrogen yield is higher if the phytotelma community is restricted to bacteria alone than when the full food web is present. Nitrogen availability is negatively affected by bacterivores (rotifers and protozoa mostly) and positively affected by a cascading effect of mosquito larvae.

4. When sedimentation rate is high, mosquitoes have a global positive effect on nitrogen production because they indirectly reduce the amount of nitrogen lost through sedimentation more than they export nitrogen through pupation. On the other hand, when sedimentation rate is low there is a hump-shaped relationship between the uptake rate of bacterivores by mosquito larvae and the nitrogen yield in the plant.

5. We conclude that plant–bacteria and plant–mosquito interactions are predominantly mutualistic, whereas plant–bacterivore interactions are predominantly parasitic. Our work also illustrates how ecosystem properties (here nitrogen production by the phytotelma community) can be understood as a function of trophic complexity and can be seen as a product of selection at the scale of a community.

Key-words: carnivorous plants, decomposition, mutualism, model, parasitism, stoichiometry, trophic cascades

Introduction

Carnivorous plants have been of interest to ecologists at least since early studies by Darwin (1875). For the plant, carnivory is considered to be an alternative way to obtain nutrients that are normally taken up from the soil through the root system. Most carnivorous plants live in nutrient-poor soils and may get a significant portion of their nutrients from capturing insects and other small invertebrates with their leaves (Juniper, Robins & Joel 1989). Although few detailed studies exist, it has been estimated that carnivorous plants get between 10% and 80% of their nitrogen budget from prey decomposition (Ellison & Gotelli 2001). Some plants produce digestive fluids to break up prey (Juniper *et al.* 1989; Gallie & Chang 1997), releasing nutrients that are then absorbed by the plant. However, in many plants, nitrogen is made available by the bacterial decomposing of prey. Invertebrates living inside the plants may also help bacterial decomposition by fractionating the dead material into smaller pieces (Heard 1994), making nitrogen more readily available to the bacteria. Thus, understanding nutrient dynamics of carnivorous plants must include an understanding of the other species associated with the plant.

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Fig. 1. The pitcher plant *Sarracenia purpurea* in the field. Photo by Nicolas Mouquet at Sumatra Savannah in the Apalachicola National Forest (USA).

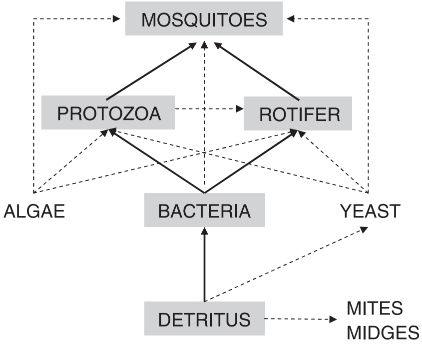

Fig. 2. Hypothetic food web of the phytotelma community inhabiting the leaves of the carnivorous plant *Sarracenia purpurea*. Based on Cochran-Stafira & von Ende (1998) and Kneitel & Miller (2002). Grey boxes and bold arrows show the simplified food web we have selected to build our model (eqns 1 and 2).

One of the best studied carnivorous plant systems is found with the northern pitcher plant, *Sarracenia purpurea* L. (Fig. 1). The water-filled leaves of this species host a small community (Fig. 2): the food web includes bacteria and midges as the primary consumers of prey captured by the leaves, protozoa and rotifers as bacteriovores, and mosquitoes acting as top predators and potential omnivores. However, while this food web has been well-studied (see Bradshaw & Creelman 1984; Miller & Kneitel 2005), the relationship between the plant and its inhabitants remains poorly understood. The inhabitant community as a whole and the constituent species may be viewed as mutualists, parasites or commensualists (Bradshaw & Creelman 1984; Heard 1994; Ellison & Gotelli 2002). While the bacteria are obviously important to the plant for decomposing detritus and the plant is obviously necessary to the phytotelma community as a host, the effect of the other trophic levels on plant fitness (mutualism, parasitism or commensalisms) is less clear. Some authors have even challenged the importance of carnivory, arguing that *S. purpurea* may in some cases get fewer nutrients from decomposing prey than from the soil (Chapin & Pastor 1995) or rainfall (Ellison & Gotelli 2002). But why, if not for carnivory, would a plant produce such a costly device as a pitcher-shaped leaf? Thus, to a larger extent, the questions of the benefit and cost of carnivory, both from ecological and evolutionary aspects, remain under debate (Ellison & Gotelli 2001).

This debate illustrates the need for a simple theoretical framework to explore both the questions of nitrogen production within carnivorous plants and the nature of the interaction between phytotelmata communities and carnivorous plants. To this purpose, we built a mechanistic model of the food web inhabiting the leaves of *S. purpurea*. While the model is somewhat preliminary, we feel it will allow us to begin to address a number of questions associated with carnivory, while pointing the way for further research and theory. We focused on nitrogen and carbon fluxes within the system because they are the basis of the interaction between the community and the plant, and between the different components of the community. Our model is stochiometric because this is the most adequate formalization of nutrient fluxes within trophic communities of interacting organisms (Sterner & Elser 2002). Mathematical analyses, numerical simulations and a nutrient budget based on parameters measured in the field and collected in the literature are used to explore several questions relative to *S. purpurea* and to carnivorous plants in general: (i) Does the system produce inorganic nitrogen? (ii) Does the plant receive more nitrogen from prey decomposition than from other sources? (iii) Does the trophic complexity affect nitrogen production? and (iv) Is the relationship between the plant and the phytotelma community mutualistic or not?

The purple pitcher plant and its phytotelma community

The purple pitcher plant *S. purpurea* is a rosette-forming perennial herb, widely distributed across low-nutrient wetlands in North America (Buckley *et al.* 2003; Ellison *et al.* 2004). Individual plants consist of several cup-shaped leaves that fill with rain water and passively capture insect prey. Insects are attracted by nectar or scent and fall and drown in the pitcher. In north Florida, the prey almost entirely consists of ants (T. Miller, unpublished results). The leaves also serve as habitat for an aquatic community called a phytotelma or inquiline community (Kitching 2000). The community consists of bacteria, protozoa, rotifers, mites and the larvae of three dipteran species, *Blaesoxipha fletcheri* (Sarcophagidae), *Wyeomyia smithii* (Culicidae) and *Metriocnemus knabi* (Chironomidae) (Fig. 2). The phytotelma community is considered to be the primary mechanism by which the plant receives nutrients from carnivory: as prey decomposes due to the activities of the community, nutrients are released into the water and absorbed by the leaf (Bradshaw & Creelman 1984; Juniper *et al.* 1989; Heard 1994, 1998). It has been previously shown that newly opened leaves of *S. purpurea* may also release some digestive fluids that act to break down insect prey (Gallie & Chang 1997). However, this secretion occurs only in the first weeks after each leaf opens (individual leaves can last longer than a year (Butler & Ellison 2007; T. Miller, unpublished results) and we will assume that its effects are generally minimal relative to the action of bacteria. Other pitcher plants, such as *S. flava*, contain little water, so that digestive fluids likely play a much larger role in prey decomposition (Christensen 1976).

The pitcher plant phytotelma community provides natural microcosms (Srivastava *et al.* 2004) that are simple enough for experimental manipulation and have been extensively utilized for understanding general properties of food webs and ecosystems (Addicott 1974; Heard 1994; Cochran-Stafira & von Ende 1998; Kneitel & Miller 2002; Miller, Kneitel & Burns 2002; Kneitel & Miller 2003; Gotelli & Ellison 2006; Gray *et al.* 2006). These studies have shown that bottom-up and top-down forces (Osenberg & Mittlebach 1996) have strong, but different, effects on the abundance of intermediate trophic levels. Bacteria are positively affected by the availability of prey and negatively affected by the direct effects of grazing by their predators (mostly rotifers and protozoa). The mosquito *W. smithii* has been suggested as a keystone predator in the pitcher community, shaping the architecture of the food web and the interaction between bacterivores and bacteria (Addicott 1974; Cochran-Stafira & von Ende 1998; Kneitel & Miller 2002).

Model presentation

The goal of our model is to describe the dynamics and balance of carbon and an essential nutrient (e.g. nitrogen or phosphorus) in an individual leaf and its constituent community. Although phosphorus is known for limiting the growth of *S. purpurea* in some cases (Wakefield *et al.* 2005), nitrogen is generally considered to be the most limiting factor (Chapin & Pastor 1995; Gray *et al.* 2006). Therefore, we will refer here to the nutrient as nitrogen, although the model and the results would hold for phosphorus as well.

We consider input and output fluxes of C (carbon) and N (nitrogen) between the pitcher community and the outside, and the internal decoupling processes through trophic interactions of species living in the pitcher. A schematic view of C and N fluxes and stocks is represented in Fig. 3. The global budget of carbon and nitrogen within the pitcher is driven by input and output fluxes. Organic C and N come into the water held in the pitcher through prey biomass, and some inorganic N (NH_4 and NO_3) comes in by atmospheric deposition (Ellison & Gotelli 2002). Organic C and N are decoupled through mineralization along the trophic chain: organic carbon is respired by the organisms in the leaf (e.g. bacteria, protists, insects, etc.) and generally exits the pitcher as CO_2, while organic nitrogen is excreted to maintain homeostasis. Excretion occurs in mineral form or in simple organic form readily available to the plant (Sterner 1990). For simplicity we will refer to the pool of mineral and readily available organic nitrogen as 'available nitrogen'.

A portion of organic N and C exits the system coupled in mosquito biomass after pupation. In addition, some detritus escapes decomposition in the water column, sinks to the bottom of the pitcher, and forms an anaerobic layer of sediment that decomposes only very slowly. We assume that over the lifetime of a pitcher leaf, the release of nutrients due to anoxia in the sediment is negligible compared to nutrients released through aerobic decomposition. Therefore, the sediment that accumulates contains C and N that is mostly unavailable to the plant and to the phytotelma community; sedimentation can be considered as an output flux.

Our model incorporates the dynamics of detritus, bacteria, bacterivores (protozoa and rotifer) and mosquito larvae. We have simplified the food web (Figs 2 and 3) as a linear system, with bacteria feeding on the detritus, rotifers and protozoa feeding on bacteria and consumed in turn by mosquito larvae. We do not consider midges and mites since they are often relatively rare (at least in southern populations that we use as an example system here) and are largely a phenomenon of older leaves (Miller & Kneitel 2005; T. Miller unpublished results); their effect on decomposition is explored in the Discussion, along with the consequences of bacteria predation by mosquitoes. Finally, while phytotelmata communities are known to go through a distinct successional pattern (Miller & Kneitel 2005) over the lifetime of a pitcher, we have chosen to simplify our model by considering a period of relative stasis.

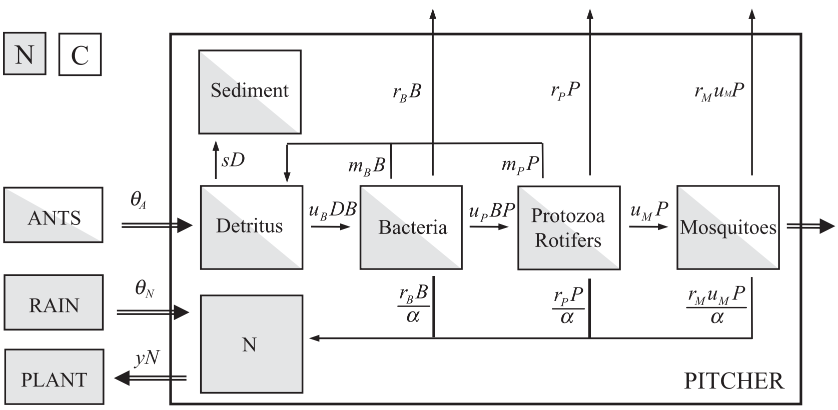

Fig. 3. Model of carbon (white boxes) and nitrogen (grey boxes) cycling in an ecosystem consisting of a carnivorous pitcher plant and its phytotelma communities. The two nutrients are always coupled (C : N = α) but we have represented only one of them for simplicity. Parameters are defined in Table 1, equation are given in the text (eqns 1 and 2).

The biotic compartments (bacteria, rotifers, protozoa and mosquito larvae) contribute to the detritus through mortality and to the available nitrogen compartment through excretion. Detritus are decomposed by bacteria, while mosquitoes are constantly filter-feeding on bacterivores (Bledzki & Ellison 1998). While this is a somewhat simplified food web (as compared with Fig. 2), it allows analytic tractability while still capturing the most important trophic characteristics of the community (prey decomposition, predation, cascading effects and stoichiometry of C and N). For simplicity, we make the rough assessment that the C : N ratio in biomass is constant and use the same ratio in detritus (mostly ants), bacteria, bacterivores and mosquitoes, although we acknowledge that slight differences are known to occur among these groups (Reiners 1986). Including differences of C : N ratios would not change the mechanism of mineralization; it would only quantitatively change the fraction of N recycled per atom of C respired. This would have introduced more complexity for minimal functional gain in the model. We assume that the uptake of available nitrogen by *S. purpurea* is linearly proportional to the concentration of available nitrogen in the pitcher.

The model accounts for the fact that the dynamics of mosquitoes and sediment occur at a different time scale than the dynamics of microorganisms. This decoupling is implemented by using dynamic equations for microorganisms, detritus pool and available nitrogen and considering mosquitoes and sediment as an external constraint for this dynamical system. During the lifetime of a leaf (several months; Miller & Kneitel 2005), mosquitoes lay eggs and some larvae develop, pupate and fly away. On the other hand, the generation times of bacteria and bacterivores are on the order of several hours, and biomasses can reach steady-state dynamics in a few days. In the same vein, the detritus and the sediment experience two different dynamics during the lifetime of a leaf. The detritus is in the aerobic bottom portion of the leaf and is effectively consumed by the food web and mineralized. Sediments are mostly composed of fine particles of chitin (mostly from ants), remnants of frass and moulted exoskeletons from mosquitoes and midges, and sometimes small amounts of sand and dirt that blow into the leaf. Sediments are not easily decomposed and represent a net loss of nitrogen for the pitcher; denitrifrying bacteria may break down these sediments through anaerobic respiration. Sediment accumulates all leaf-life long, and a leaf may contain a significant amount of sediment at the time of its 'death' (T. Miller, personal observation). The amount of sediment that accumulates depends on the rate at which bacteria can process detritus before it sinks and becomes anaerobic.

The dynamics for key components of the community are modelled as:

$$\begin{aligned} \dot{D} &= \theta_A + m_B B + m_P P - u_B DB - sD \\ \dot{B} &= u_B DB - (m_B + r_B)B - u_P BP \\ \dot{P} &= u_P BP - (m_P + r_P)P - u_M P \\ \dot{N} &= \theta_N + \frac{r_B B + r_P P + r_M u_M P}{\alpha} - yN \end{aligned} \qquad \text{(eqn 1)}$$

Where D is the detritus (expressed in atoms of C), B is the bacterial population (expressed in atoms of C), P is the bacterivores population (in atoms of C), and N is the pool of available nitrogen within the pitcher (in atoms of N). The dot above the variable denotes a derivative with respect to time. θ_A is the carbon input flux from detritus. m_B, m_P, r_B, r_P, u_B and u_P are, respectively, the bacteria and bacterivores mortality (*m*), respiration (*r*) and consumption rates (*u*). *s* is the sedimentation rate. u_M is the mosquitoes predation rate. θ_N is the flux of inorganic nitrogen coming with rainwater. α is the C : N ratio in the organic matter. *y* is the uptake rate of nitrogen by the plant. Parameters definition and units are in Table 1 and Fig. 3.

In addition, two equations account for the dynamics of the sediment and mosquitoes that occur at a much slower rate (as explained above).

$$\begin{aligned} \dot{Se} &= sD \\ \dot{Mo} &= u_M P(1 - r_M) \end{aligned} \qquad \text{(eqn 2)}$$

Where *Se* represents the sediment (expressed in atoms of C), *Mo* represents the biomass of mosquito larvae (expressed in atoms of C) and r_M is the mosquito larvae respiration rate. The yield $u_M P$ of bacterivores by mosquito larvae depends on bacterivore abundance (expressed by the biomass P) and the mosquito predation rate u_M is their per-capita uptake rate times the number of mosquito larvae. We assume that since mosquito larvae are in a growing phase in the pitcher, they mostly accumulate biomass and therefore produce negligible detritus. The functional response is assumed to be linear for analytical simplicity and reflects the fact that in real pitchers the densities of bacterivores may never saturate the mosquitoes (i.e. the per-capita uptake rate is constant).

Note that eqn (2) cannot equal zero for non-null values of detritus D and bacterivores P. Indeed, the sediment and mosquito compartments are not considered to be at equilibrium during the time period considered with this model (1). Therefore, sedimentation and accumulation of matter in mosquito biomass are considered as a net export.

Parameters estimation

Details of parameter estimation are given in Appendix S1 in Supplementary Material with values in Table 1. Model parameters were estimated in the field where possible and supplemented by data from the literature. Parameters that were not found in the literature were estimated with ad-hoc parameterization by solving the equations with steady-state biomass measured in the field for each compartment. Most field data come from sites located in the Apalachicola National Forest in north Florida, USA.

Results

COMPARTMENTS AT EQUILIBRIUM

The model shows the following non-trivial equilibrium where all the compartments are positive. As most healthy leaves will

Table 1. Symbols used in the text and equations, dimensions and values used for simulations (see Appendix S1 for details)

	Definition	Dimension	Values
Variables			
B	Bacteria biomass	mg of C L^{-1}	5·00
D	Detritus biomass	mg of C L^{-1}	371·25
N	Nitrogen concentration	mg of C L^{-1}	0·817
P	Bacterivores biomass	mg of C L^{-1}	27·85
Se	Sediments biomass	mg of C L^{-1}	None
Mo	Mosquitoes biomass	mg of C L^{-1}	303·75
Parameters			
α	C : N ratio in the organic matter	None	6·625
θ_A	Carbon input flux from detritus	mg of C L^{-1} day^{-1}	5·39
θ_N	Flux of inorganic nitrogen coming with rainwater	mg of N L^{-1} day^{-1}	0·0751
m_B	Bacteria mortality rate	day^{-1}	0·001
m_P	Bacterivores mortality rate	day^{-1}	0·01
r_B	Bacteria respiration rate	day^{-1}	0·0005
r_P	Bacterivores respiration rate	day^{-1}	0·0014
r_M	Mosquitoes respiration rate	day^{-1}	0·01
s	Sedimentation rate	day^{-1}	0·01
u_B	Bacteria consumption rate of detritus	day^{-1} mg of C^{-1}	0·001
u_P	Bacterivores predation rate	day^{-1} mg of C^{-1}	0·014
u_M	Mosquitoes predation rate	day^{-1}	0·5872
y	Uptake rate of nitrogen by the plant	day^{-1}	0·1026

have bacteria, protozoa, mosquitoes and detritus, this should correspond to the situation generally found in natural pitchers. The star denotes the value of a variable at equilibrium:

$$B^* = \frac{m_P + r_P + u_M}{u_P}$$

$$P^* = \frac{u_B(\theta_A - r_B B^*) - s(m_B + r_B)}{u_B(u_P B^* - m_P) + s u_P} \qquad \text{(eqn 3)}$$

$$D^* = \frac{m_B + r_B + u_P P^*}{u_B}$$

$$N^* = \frac{\alpha\theta_N + r_B B^* + (r_P + r_M u_M)P^*}{y\alpha}$$

The global balance of nutrients within the pitcher is driven by the inputs: ants for carbon, and ants and rainwater for nitrogen, and the outputs: respiration, exports by mosquitoes and plant yield. For each transfer of organic matter from one trophic level to the other there is a net mineralization of carbon through respiration (see eqn 1 and Fig. 3) with a subsequent fraction of nitrogen rejected in its available form. Thus, the whole pitcher is a mineralizing system that produces nitrogen that is finally available for the plant. However, its efficiency is limited, since part of the organic nitrogen that comes to the pitcher with ants is lost by sedimentation or exported from the system through mosquito pupation. At equilibrium (1), we define the gain of available nitrogen G from the ants as the input flux of detritus minus the two paths of loss (namely, sedimentation and export by mosquitoes):

$$G = \frac{1}{\alpha}(\theta_A - sD^* - (1 - r_M)u_M P^*) \qquad \text{(eqn 4)}$$

G is a flux of nitrogen, expressed in mg N day^{-1}. Note that, as mentioned earlier and by virtue of respiration, the community releases available nitrogen from the detritus. Therefore, since we assume that there is no outlet for available nitrogen other than the plant's uptake, the gain G has to be positive. Indeed, after some algebra with eqn (4) it turns that:

$$G = yN^* - \theta_N = \frac{r_B B^* + (r_P + r_M u_M)P^*}{\alpha} \qquad \text{(eqn 5)}$$

Therefore, as long as the bacteria and bacterivores sustain positive biomass at equilibrium, the gain G is positive. The community produces nitrogen for the plant whatever the amount of detritus input.

EFFECT OF TROPHIC COMPLEXITY AND SEDIMENTATION ON NITROGEN AVAILABILITY

From the global sensibility analysis given in Table 2, the gain G of nitrogen for the plant increases with the detritus input and with the uptake rate of detritus by bacteria. On the other hand, the uptake rate of bacteria by bacterivores and the sedimentation rate have a negative effect on G. The effect of the uptake rate of bacterivores by the mosquitoes is less trivial (hump shaped) and depends on the magnitude of the sedimentation rate. The model suggests that the level of trophic complexity (i.e. the number of trophic levels) and the sedimentation rate are key factors that influence the nitrogen availability within each leaf.

Although it is clear that the plant is getting nutrients from prey decomposition of the detritus by the food web inhabiting its leaves, it is less clear how the constitution of the phytotelma

Table 2. Sensibility analysis for the principal parameters used in our model. We have considered the cases with ($s > 0$) and without sedimentation ($s = 0$) and noted the results when they were different

Parameters	Detritus	Bacteria	Bacterivores	Nitrogen	Gain
Mosquito uptake u_M	(–)	(+)	(–)	(+/–) if $s = 0$ (+) if $s > 0$	(+/–) if $s = 0$ (+) if $s > 0$
Detritus input θ_A	(+)	0	(+)	(+)	(+)
Nitrogen input θ_N	0	0	0	(+)	0
Bacteria uptake u_B	(–)	0	0 if $s = 0$ (+) if $s > 0$	0 if $s = 0$ (+) if $s > 0$	0 if $s = 0$ (+) if $s > 0$
Bacterivores uptake u_P	(+)	(–)	(+) if $s = 0$ (–) if $s > 0$	(–)	(–)
Plant uptake y	0	0	0	(–)	0
Sedimentation s	(–)	0	(–)	(–)	(–)

community affects the gain G of nitrogen for the plant. To address this question, it is necessary to consider the effects of trophic complexity step by step, starting with the simplest level with bacteria alone, then with bacteria and bacterivores, to finish with the full chain with bacteria, bacterivores and mosquitoes:

(1) Bacteria alone:

$$B^* = \frac{\theta_A - sD^*}{r_B}$$

$$D^* = \frac{m_B + r_B}{u_B} \qquad \text{(eqn 6)}$$

$$N^* = \frac{\alpha\theta_N + r_B B^*}{y\alpha}$$

$$\text{gives: } G = \frac{1}{\alpha}(\theta_A - sD^*) \qquad \text{(eqn 7)}$$

(2) Bacteria and bacterivores:

$$B^* = \frac{m_P + r_P}{u_P}$$

$$P^* = \frac{u_B(\theta_A - r_B B^*) - s(m_B + r_B)}{u_P(u_B B^* - m_P) + su_p}$$

$$\text{(eqn 8)}$$

$$D^* = \frac{m_B + r_B + u_P P^*}{u_B}$$

$$N^* = \frac{\alpha\theta_N + r_B B^* + r_P P^*}{y\alpha}$$

$$\text{gives: } G = \frac{1}{\alpha}(\theta_A - sD^*) \qquad \text{(eqn 9)}$$

Note that while this appears similar to eqn (7), G is higher with bacteria alone than with bacteria and bacterivores, because bacterivores increase the mortality rate of bacteria and thus decrease the efficiency of prey decomposition (D^* is higher).

(3) Bacteria, bacterivores and mosquitoes: see eqns (3)–(5)

The effect of mosquitoes on a system with bacteria and bacterivores is not trivial. As mentioned earlier the uptake rate u_m of bacterivores by mosquitoes is the per-capita uptake times the number of mosquito larvae within the pitcher. Therefore, the higher the number of larvae in the pitcher, the higher the parameter u_m.

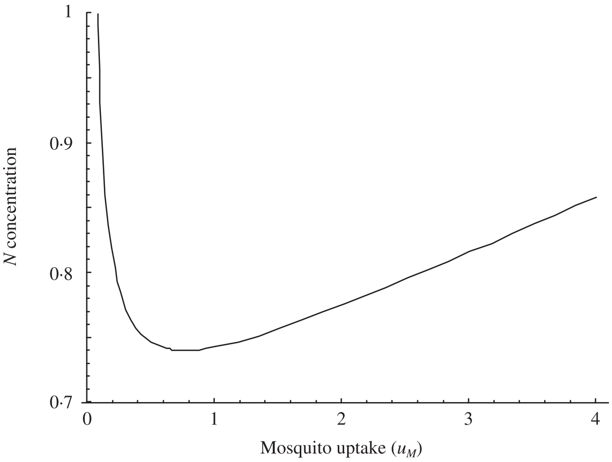

Fig. 4. Effect of the mosquito uptake u_M on available nitrogen concentration at equilibrium within the pitcher plant when the sedimentation rate is zero ($s = 0$). Parameters are defined in Table 1, equation are given in the text (eqns 1 and 2).

With no sedimentation, the addition of mosquitoes will have a pure negative effect on G; that is, G is lower with mosquitoes (eqn 4) than without mosquitoes (eqn 9; Fig. 4). This results from the fact that mosquitoes represent only a loss of nitrogen from the system (1), which is represented by the subtracted term$(1 - r_M)u_M P^*$ in eqn (4). However, if mosquitoes are present ($u_M > 0$), increasing their density might have an opposite effect on the magnitude of the loss of gain G (and thus on nitrogen production as illustrated in Fig. 4). This is due to a density-dependence, or 'self-shading effect' of mosquitoes. At low density, an increase of mosquito numbers increases the predation effort on bacterivores without reducing much of the bacterivores' density. It results in a net increase of the flux of biomass transferred between the two trophic levels. On the other hand, at higher densities the positive effect of the predation effort is overwhelmed by the decrease of the bacterivores' density, and the net effect is a decrease of the biomass transfer. In other words, with no sedimentation it is better for the plant not to have mosquitoes but once they are present it is better to have a lot of them.

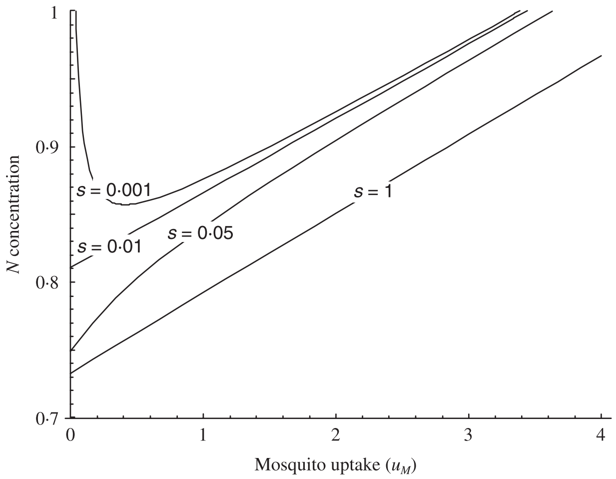

Fig. 5. Effect of the mosquito uptake u_M on available nitrogen concentration within the pitcher plant at equilibrium when the sedimentation rate is positive ($s > 0$). Parameters are defined in Table 1, equations are given in the text (eqns 1 and 2). To make comparison possible, the parameters have not been recalculated (see Appendix S1) for each value of s but have been chosen on the basis of $s = 0{\cdot}01$ (for this reason the curve obtained with $s = 0{\cdot}001$ is much higher than what expected from the Fig. 4).

With sedimentation, the interaction is more complex as the effect of mosquitoes on prey decomposition is related to the sedimentation rate s (Fig. 5). Indeed, sedimentation, which depends on the level of detritus D^* in the pitcher (the loss is expressed by the term sD^* in eqns 4, 7 and 9), results in a loss of nitrogen to the plant. By cascading effects, bacterivores increase D^* while feeding on bacteria (see the expression of D^* in eqn 8 compared to eqn 6). As a consequence, they increase the flux of detritus that goes to sedimentation, resulting in a decrease in G for the plant. In this competitive arena between the gain G and the sedimentation, mosquitoes act through two mechanisms: first, as described in the former paragraph, they create an additional loss path for nitrogen. Second, by a cascading effect, they reduce bacterivores' density, hence increase bacterial biomass, which results in a better control of detritus biomass D^*, preventing losses through sedimentation. The first mechanism has a negative effect on G, whereas the second mechanism is positive. The overall effect can be either positive or negative depending on the sedimentation rate s. From G one can obtain the threshold value of s_{limit} for which the global impact of mosquitoes switches from a purely negative hump-shaped effect to a purely positive effect by setting the derivative dG/du_M to zero. It becomes:

$$S_{limit} = \frac{1 - r_M}{r_M} \times \frac{u_B}{u_P} r_P \qquad \text{(eqn 10)}$$

For $s < s_{limit}$ the global impact of mosquitoes on nitrogen production is negative, dominated by exportation. For $s > s_{limit}$ there is a pure positive effect of mosquitoes on G, dominated by the cascading effect (Fig. 5). Note that this positive effect is more pronounced for low to intermediate values of mosquito density because, as bacterial control of detritus has reached a maximum, the additional increase on G is only due to a decrease in the negative effect through exportation.

Discussion

DOES THE SYSTEM PRODUCE AVAILABLE NITROGEN?

Our simple model predicts that the community found in the leaves of pitcher plants is a mineralizing system that produces nitrogen which is then available to the host plant. While this is only a first attempt at modelling this system and our work is somewhat exploratory, our results provide significant insight into the potential interactions in this system. Respiration by the different constituents of the food web inhabiting the leaf insures a minimum level of nitrogen excretion as long as any prey is captured by the leaf. Mosquitoes have the potential to be parasites on this system, as adults export nitrogen from the system when they leave the pitcher. However, we have included losses through mosquito departure and sedimentation, and our results show that nitrogen production is always positive (eqn 5). In fact, nitrogen production may even be enhanced by the presence of mosquitoes, due to their effects on bacteriovores (Fig. 5).

We have also not considered any denitrification in our model, which would likely lead to a net loss of nitrate for the pitcher. Denitrification occurs when oxygen concentrations are low, causing some bacteria to turn to nitrate in order to respire and decompose organic matter. Nitrate is then transformed into atmospheric nitrogen ($2NO_3^- + 10e^- + 12H^+ \rightarrow N_2 + 6H_2O$) that cannot be used by the plant. Oxygen is a more favourable form of electron acceptor than nitrate and denitrification will only occur in poorly aerated parts of the pitcher. Denitrification probably does occur in the sediment accumulated at the bottom of the pitcher and might become dominant when the sediment reaches a threshold value. We have observed some evidence of denitrification, with pitcher water occasionally turning to red-brown and becoming viscous and fetid: however, this is a rare event in natural populations and difficult to create in the laboratory (T. Miller, personal observation; Bradshaw & Creelman 1984). While sediments are frequently observed in natural leaves, we have no data on sedimentation rate within the pitcher and our model has not been built to find sediment biomass at equilibrium.

There are several other inquiline species that are common in some populations of *S. purpurea*, but not included in this version of the model. We have chosen to focus on common species or groups of species that are generally abundant in all *S. purpurea* populations; but we can speculate on the roles of some of these neglected species. Larvae of midges (*M. knabi*) feed on accumulated insects at the bottom of the leaf chamber while larvae of flesh flies (*Fletcherimyia fletcheri*) attack and consume prey when they first fall in the water. Both may have indirect effects on other species by shredding prey and promoting bacterial productivity (see, Heard 1994). Both species should have a simple positive direct effect in the available nitrogen production since they eat detritus and release available nitrogen through excretion. By eating detritus and moving the sediments, midges may also make more oxygen available to bacteria and thus delay denitrification. They also have a potential negative effect on the bacteria by eating them with the detritus. Some experimental studies have found a positive relationship between midge presence and bacterial densities (Trzcinski, Walde & Taylor 2005) suggesting that they have an overall positive effect on bacterial activity and thus on available nitrogen production. However, both of these dipterans are relatively rare in southern populations and are primarily a phenomenon of older leaves (Miller & Kneitel 2005, T. Miller unpublished results). The full role of these dipterans remains to be investigated and perhaps integrated into later versions of our model.

In the same vein, the consumption of bacteria by mosquitoes should tend to dampen the positive cascading effect of mosquitoes on bacterial density. However, it is likely that the overall cascading effect would remain positive because mosquitoes are less efficient than fast growing protists in controlling bacterial density (T. Miller, personal observation).

DOES *SARRACENIA PURPUREA* RECEIVE MORE NITROGEN FROM PREY DECOMPOSITION THAN FROM OTHER SOURCES OF NITROGEN?

Although it has been estimated that carnivorous plants can obtain up to 80% of their N and P uptake from decomposing prey (Juniper *et al.* 1989), the question of whether they really benefit from or require prey capture is still open (Adamec 1997; Ellison & Gotelli 2001; Ellison 2006; however, see Farnsworth & Ellison 2008). Clearly, there is a large range of carnivory strategies (from almost total dependence to relative independence of prey) and high variability in the responses within single species to environmental variation to prey and nutrient addition (Adamec 1997). Pitcher plants have many potential sources of nitrogen, either directly from the soil, from decomposing their prey, from rain water deposition within the leaf (Ellison & Gotelli 2002), or even from atmospheric nitrogen fixed by bacteria in the leaves (Prankevicius & Cameron 1991).

To understand how much nitrogen *S. purpurea* might really get from prey decomposition, we can use the available data and our model to compare the input of nitrogen from the different sources available to the plant (Appendix S2 in Supplementary Material). Based on these different numbers, it appears that decomposition of prey may provide perhaps one-third to half the nitrogen for *S. purpurea*. This is consistent with at least one previous, admittedly broad, estimate that carnivorous plants could get from 10% to 80 % of their nitrogen through prey capture (Juniper *et al.* 1989). Obviously, these are very general estimates that will depend greatly on environmental conditions (soil pH, prey availability, atmospheric deposition). Chapin & Pastor (1995) have shown that *S. purpurea* could get as little as 10% of its nitrogen budget from decomposition of insects trapped within its leaves, the other 90% coming from the soil or rain water. They added prey to the pitcher and found no effect on the number of leaves produced or leaf biomass within the growing season. They concluded that *S. purpurea* was getting little of its nutrients from prey capture. However, as shown by Wakefield *et al.* (2005), prey addition might have no effect on 'traditional' measures such as leaf morphology, growth and photosynthetic rates, but strong effects on nutrient limitation. They have shown that prey addition in leaves of *S. purpurea* shifted these plants from P to N limitation. These synergistic effects have been found in other carnivorous plants (Hanslin & Karlsson 1996; Adamec 2002) and illustrate that the nutrient absorption in carnivorous plants is complex, making the interpretation of prey addition experiments such as done by Chapin & Pastor (1995) difficult. Thus, the question of whether carnivorous plants may benefit from prey capture is still open, but at least the numbers we have found make clear the high potential of nitrogen uptake to contribute to the overall plant nutrient dynamics.

TROPHIC COMPLEXITY AND NITROGEN PRODUCTION?

We have shown that the plant may obtain more nutrients when only bacteria are present than with the full food web. However, when there are other species than bacteria alone it is better to have a complex trophic structure (as described in Fig. 2) than a simple consumer (bacteria)–predators (bacterivores) loop. Bacteria are negatively affected by the direct effect of grazing by their predators (mostly protozoa and rotifers) and positively affected by a cascading effect of predation by large numbers of mosquito larvae. Despite the fact that protozoa and rotifers could excrete significant amounts of nitrogen within the leaf (Bledzki & Ellison 1998), our model suggests that their effect on N availability to the plant may be globally negative. Predation on bacteria decreases bacterial density, which reduces the fraction of organic matter that is processed before sedimentation. Bacteriovores may have some positive effects not included in our model, perhaps by moving the detritus or the sediments and increasing prey decomposition rates, but we still believe that bacterivores have a net negative effect on the nitrogen production. Predation on bacteriovores by mosquitoes increases the rate of organic matter decomposition by decreasing the bacterivores' density. On the other hand, each mosquito that pupates and leaves the leaf is a net loss of nitrogen from the pitcher. So, our model predicts contrasting effects of mosquito larvae, depending on the sedimentation rate. When the sedimentation rate is high, mosquitoes have a global positive effect on nitrogen production because they indirectly reduce the amount of nitrogen lost through sedimentation (by indirectly increasing bacteria density and thus detritus consumption) more than they export nitrogen through pupation.

Our results are consistent with experiments that have manipulated mosquito larvae density and found a negative effect on bacterivores and a positive effect on bacteria (Kneitel & Miller 2002). Note that the positive effect of mosquitoes on bacteria through this trophic cascade may be influenced by omnivory of mosquitoes feeding directly on bacteria (Cochran-Stafira & von Ende 1998; Kneitel & Miller 2002). There are other potential positive effects of the mosquitoes on the decomposition loop within the leaf. For instance, both Cochran-Stafira & von Ende (1998) and Kneitel & Miller (2002) found that feeding by the mosquito *W. smithii* changed the composition of the bacteriovore community and species-specific differences among the bacteriovores could affect aspects of nutrient recycling (DeAngelis, Post & Travis 1986). Also, excretion of detritus by mosquitoes during their development (moulting) could have a global positive effect of the nitrogen production. Recent experiments with a Bromeliad ecosystem (Ngai & Srivastava 2006) have shown that, in the presence of top predators, there was an enrichment in N compared with plants containing detritivores alone. This result is consistent with our analyses and shows how our results can be interpreted in a broader context.

Trophic complexity leads to indirect effects in food webs (DeAngelis 1992), which have been proposed to increase ecosystem functioning (Thebault & Loreau 2006). For instance, de Mazancourt, Loreau & Abbadie (1998) have shown that the complexity of a plant–herbivore–decomposer food web could lead in some cases to a kind of mutualism between a plant and an herbivore, if the proportion of nutrients lost along the herbivore pathway is sufficiently smaller than the proportion of nutrient lost through the rest of the ecosystem. A similar situation occurs in our model: when the proportion of nutrients lost along the predation pathway (export through pupation) is smaller than the proportion of nutrients lost through sedimentation, there is an overall positive effect of mosquito larvae predation. Complex food webs 'accelerate' fluxes of nutrients within the ecosystem and lead to a lower net loss of nutrients (e.g. sedimentation, leaching) which, virtually by definition, results in increased ecosystem function. This result must be interpreted cautiously since the relationship between trophic complexity and ecosystem functioning is non-linear (Thebault & Loreau 2006) and depends on what function is considered (e.g. optimizing nutrient production and retention or temporal stability at the various trophic levels will necessarily need different mechanisms). Our work illustrates one of these effects; showing how trophic complexity can enhance nitrogen production within a simple ecosystem such as the phytotelma community.

MUTUALISM AND EVOLUTION

Our results provide some insight into the potential mutualism between the pitcher plant and the phytotelma community inhabiting its leaves. Bacteria do appear to be mutualists, since they are needed for the plant to decompose prey and obtain nutrients, while the plant is needed by the bacteria both as a habitat and a source of organic matter. This association might even be stronger if the plants secrete any enzymes to break down organic matter, which may increase the rate of prey decomposition by bacteria (Gallie & Chang 1997). It is less clear if bacterivores and mosquitoes individually are mutualists, since we have shown that the community may produce less nitrogen when they are present but that together, their contributions to trophic complexity (presence of both bacterivores and mosquito larvae) leads to a potential positive effect of mosquitoes at certain abundances on nutrient production.

Plants are known to produce root exudates (mixture of sugars, vitamins, amino acids, inorganic ions and other elements) to activate bacterial activity and nitrogen recycling in the vicinity of their roots (Dakora & Phillips 2002). The evolution of a mutualism between the pitcher plant and the bacteria could also include such 'enhancer effects', with the plant trading carbon for nitrogen with the phytotelma community. The bacteria found in pitcher plant leaves have been shown to be carbon limited (Gray *et al.* 2006). Any amount of sugar released in the pitcher by the plant would thus increase the amount of detritus decomposed by the bacteria and increase nitrogen production. This cannot be directly implemented into our model since we do consider that carbon and nitrogen are coupled but it would correspond basically to increasing the detritus input and thus would lead to increased nitrogen production (Table 2). This would not mean a real 'control' of the phytotelma community by the plant but at least some kind of 'enhancer effect' somewhat comparable to the production of enzymes that are at the basis of prey decomposition in some other carnivorous plants (Juniper *et al.* 1989). We could not find any evidence in the literature of pitcher plants excreting any sugar within their leaf to this purpose, but they may produce nectar at the leaf lip, which suggests the potential for leaves to stimulate their bacterial community. Further work is needed to investigate this possibility.

We also do not know whether the plant and its phytotelma community are the result of some sort of co-evolution or if it could be achieved by each species evolving independently (Bradshaw & Creelman 1984). However, studies of the geographic distribution of species of the phytotelma community inhabiting the leaves of *S. purpurea* show a high consistency in taxa identity as well as the trophic organization over a large spatial scale (spanning 30° of latitude and 70° of longitude), despite strong environmental and climatic variation (Buckley *et al.* 2003). Treehole communities, with similar structure to pitcher plant phytotelmata, demonstrate significant variation across similar ranges (Srivastava 2005). This surprising stability of phytotelmata communities within the pitcher plant suggests that the community and its trophic structure may have been selected at some level, perhaps because of some stability related to the overall pattern of nutrient exchange. In that case, it is more a 'mutualism' between the plant and a particular configuration of a community rather than with any particular species. This illustrates how a higher level of selection (the plant is the unit of selection for the phytotelma community) might shape the structure and trophic complexity of a whole ecosystem. This last point is very speculative; more elements might come from other large scale studies of distributions of species hosted in living habitats as well as more detailed studies of the phylogeny of species inhabiting the leaves of the phytotelma.

Acknowledgments

We would like to thank Nicholas Gotelli and Steve Heard and for providing helpful comments on earlier version of our manuscript. Bill Bradshaw for general advices. Jamie Kneitel kindly provided us with some data to parameterize our model. We thank Pr. D. Raubenheimer, L. Adamec, and two anonymous reviewers for comments on the manuscript. This research was funded in part by the National Science Foundation (DEB 0091776 to T.E.M.).

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Received 29 October 2007; accepted 03 April 2008
Handling Editor: David Raubenheimer

Supplementary material

The following supplementary material is available for this article:

Appendix S1. Details on parameter estimation.

Appendix S2. Nitrogen budget for the plant.

This material is available as part of the online article from:
http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2745.2008.01421.x
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