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Review

Nepenthes: State of the art of an inspiring plant for biotechnologists

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ABSTRACT

Plant carnivory results from the adaptation of plants to their environment. The capture and digestion of preys, followed by their assimilation by the plant is a source of additional nutrients to overcome scarce nutrient in poor soils. *Nepenthes* are highly studied carnivorous plants and have developed a number of ecological traits which have attracted the attention of plant biologists.

Multiple adaptive strategies developed by these plants make them a source of inspiration for many applications ranging from therapeutic treatments to biocontrol solution in agriculture. The outstanding tissue organization of the digestive pitcher can help to create new and original materials usable in everyday life.

In this review article, we propose a state of the art of the latest studies carried out on these particular plants and we establish a list of potential tracks for their exploitation.

1. Introduction

Carnivory in plants is a relatively rare phenomenon explained by an adaptation to nutrient-poor habitats and is considered as an additional pathway for acquisition of supplemental nutrients like nitrogen and phosphorus (Adamec, 1997). According to Juniper et al. (1989) a plant is defined as carnivorous through its ability to attract, catch, retain and digest preys into easily assimilated compounds and subsequently to absorb nitrogen products for its growth and reproduction (Ellison, 2006). About 600 plant species (18 genera and 8 families) belonging mainly to Caryophyllales and Lamiales have developed fascinating morphological and anatomical features linked to carnivory: flypaper-traps using an adhesive mucilage covering leaves (*Drosera*, *Pinguicula*, *Drosophyllum*), active snap-traps (*Aldrovandra*, *Dionaea*), active sucking bladder-traps (*Utricularia*) and passive pitcher-shaped traps (*Nepenthes*, *Sarracenia*, *Heliamphora*, *Darlingtonia*, *Cephalotus*).

The genus *Nepenthes* contains almost 120 species which are probably the most studied pitcher plants (McPherson, 2009). The diversity in size, in shape and in colour pattern of their pitcher has attracted interest since centuries. Each leaf base is extended by a tendril linked to a passive pitcher-shaped trap exhibiting three distinct functional areas on the inner surface (Fig. 1). The peristome corresponding to a colourful collar-shaped structure surrounding and overhanging the opening of the pitcher is involved in attracting and trapping prey (Bohn and Federle, 2004; Bauer et al., 2008;). The slippery area is coated by wax which favours trapping and prevents escape of prey (Gaume et al., 2002). The digestive area located at the bottom part of the pitchers is covered by glands which are producing an acidic viscoelastic fluid intended to retain and digest caught preys (Riedel et al., 2003; Gaume et al., 2004; Gaume and Forterre, 2007; Bazile et al., 2015). After being attracted by extra-floral nectar (Bauer et al., 2008), flower-scents (Di Giusto et al., 2010), colour contrasts (Moran et al., 1999) and UV spectral patterns (Kurup et al., 2013), insects are falling into the pitcher because of anisotropy and slippery properties of the peristome (Bohn and Federle, 2004; Gaume et al., 2004). Glands localized at the bottom of the pitcher have two complementary functions. They produce an acidic digestive fluid containing a blend of digestive enzymes, antimicrobial compounds, mineral nutrients (Buch et al., 2013) and acidic polysaccharides (Gaume and Forterre, 2007). They are also necessary for the assimilation of nutrients resulting from prey digestion (Owen et al., 1999; Adlassnig et al., 2012).

Nepenthes exhibit several ethnobotanical uses around the world. *N. ampullaria* and *N. gracilis* boiled roots are useful for curing stomach ache in Malaysian tribes. Infused parts of stems were used for fever. The plant stem provides material in housing construction and replace the function of rattan due to its plasticity and long-lasting properties. The most common use remains the source of water for thirsty hikers. In Malaysia, glutinous rice snack is prepared and sold in *N. ampullaria* pitchers as an attractive vessel option (Juniper et al., 1989; Clarke, 1997). Beyond these traditional uses, aqueous extract of N. khasiana is used with success as reducer for synthesis of gold nanoparticles from gold salts thanks to its antioxidant phytochemicals. These gold particles

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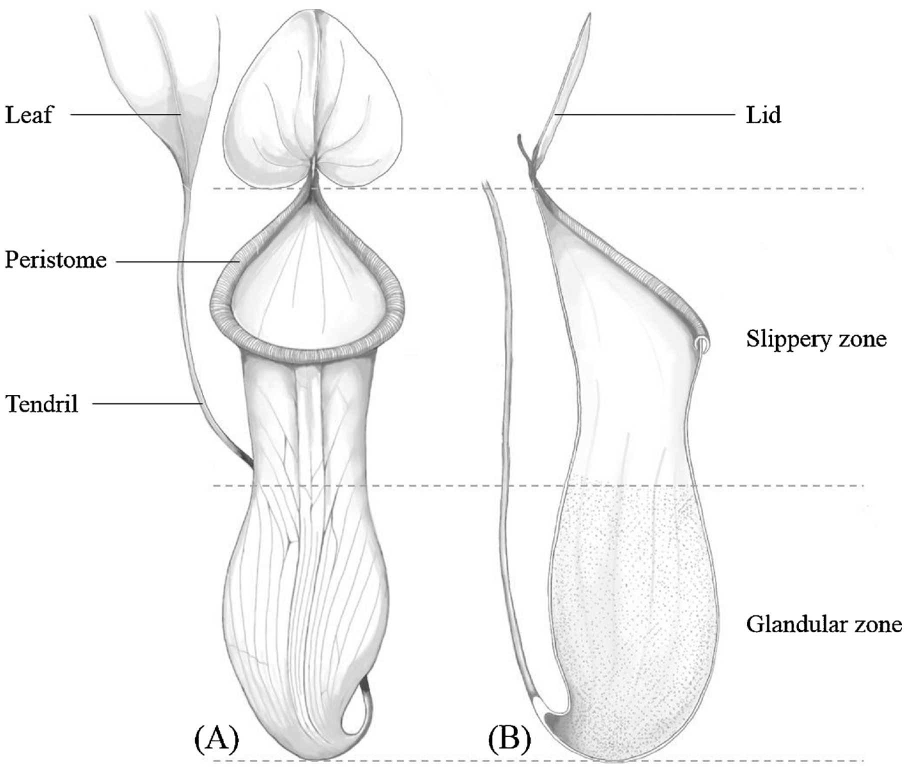

Fig. 1. *Nepenthes* pitcher organization (A) and its longitudinal section (B).

present a remarkable stability and a biocompatibility to be used as nanomedicine for diagnosis and drug therapy (Dhamecha et al., 2016).

Features linked to carnivory may also be a source of inspiration for scientists for applications in the field of biotechnology or biomimetics. In this review, we propose a survey of the scientific literature on these extraordinary plants and some possible ways to exploit their remarkable properties.

2. A tool for biotechnology and a solution for biocontrol or medical application

2.1. Proteins

The carnivorous syndrome is an important energetic investment for plants. The pool of digestive enzymes has to be efficient so that the benefits obtained from digested prey outweigh the cost of carnivory. A complex association of enzymes favouring the gain of the greatest amount of nutrients from prey degradation is therefore expected. A remarkable adaptation of these proteins to their harsh environment allows digesting preys or organic compounds. They also prevent microbial contamination in pitcher during several weeks to ensure the survival of the plant (Athauda et al., 2004). These enzymes appear to be designed such that they remain stable over wide ranges of temperature or pH. In addition, given the highly proteolytic environment of the digestive fluid, they are also resistant at different classes of proteases. Thanks to these properties, these enzymes became excellent candidates for biotechnological and therapeutic applications.

Digestive properties of Nepenthesins (aspartic proteases) are studied for medical and proteomic applications. They are more stable than porcine pepsin A and remain active several weeks at acidic pH at 37 °C (Athauda et al., 2004; Schrader et al., 2017). This stability has been reported to be related to N-glycosylation and to a higher number of disulphide bonds stabilizing the structure (Athauda et al., 2004; Kubota et al., 2010; Kadek et al., 2014b). As pepsin, nepenthesins are cleaving proteins behind hydrophobic amino acid residues and display unusual tryptic and chymotryptic properties at low pH (Rey et al., 2016). Given these remarkable particularities, *Nepenthes* secretion have recently been considered as an alternative source of therapeutic enzymes for the treatment of celiac disease triggered by gluten proteins present in common grain products (Rey et al., 2016). Within the strong acidic pH constraints of human gastric digestion, low amounts of *Nepenthes* enzymes enhance the solubilisation rate of gliadin slurries necessary for effective digestion in the stomach. When pepsin is combined to proteases present in the *Nepenthes* fluid, it is reported to be more efficient in gliadin digestion. When pepsin is associated with the single Nepenthesin 2, a surprising reduction of intestinal inflammation could be observed (Rey et al., 2016). The synergy between *Nepenthes* proteases and pepsin is obvious. AN-PEP is one of the most effective protease used in gluten-free diet to achieve gliadin digestion. To obtain the same effect than *Nepenthes* enzymes, 25 times more AN-PEP is necessary and 1000 times more proteins are recommended to achieve a comparable slurry clarification (Rey et al., 2016).

Beside these therapeutic applications, Nepenthesins 1 and 2 (rNep1 and 2) were also tested for digestion in hydrogen/deuterium exchange mass spectrometry (HX-MS) reactions. The enzymes led to the production of small and overlapping peptides allowing sufficient coverage of proteins for localizing regions of interest (Kadek et al., 2014a; Kadek et al., 2014b; Yang et al., 2015). Among both enzymes, rNep2 was demonstrated to be significantly more resistant to denaturants and reducing agents. It constitutes therefore a better choice for in-solution experiment in association with pepsin (Yang et al., 2015). Recently, new Nepenthesin variants (Nepenthesin 2-like protein/Nep3, 4 and 5) were discovered and may expand the reagent panel for potential proteomic applications (Lee et al., 2016).

Neprosin 1 is another enzyme isolated from *Nepenthes* digestive fluids and might be used as prolyl endopeptidase for a bottom-up proteomic approach. This enzyme is efficient in low pH conditions and under mild denaturing conditions. It cleaves proteins behind proline and alanine and in contrast to most proline-cleaving enzymes, it degrades proteins of any size. It is therefore complementary to conventional enzymes and may help to improve sequence coverage for whole proteome analysis and histone mapping (Athauda et al., 2004; Schrader et al., 2017).

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