The use of the right words: why carnitropism is inaccurate for carnivorous plants. Suggestion to reject the term "carnitropism"

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Abstract: In the September 2017 issue of Carnivorous Plant Newsletter, the term 'carnitropism' was proposed to name triggered movements occurring in *Dionaea*, *Drosera*, and *Pinguicula* genera. However, those phenomena were misconceived and their interpretation lacked scientific background, misleading to a flawed conclusion. Therefore, the present paper recommends to avoid the use of that term and recalls both the mechanisms behind plant movements and their associated names.

Introduction

Simón (2017) explained that "*Plants are known to move towards certain stimuli (water, light, gravity) which are beneficial and these movements have been labeled hydrotropism, phototropism, geotropism*." Yet, such a statement is very likely to bring confusion. For one thing, no definition of tropism including its physiological origin was clearly introduced in the article. A couple of examples cannot make up for that absence. For another, although tropism is indeed *an instance* of plant reaction to stimuli, that is not the sole one. Another kind of reaction, called "nastic movement" is actually more common when it comes to carnivorous plants. The main difference between these two mechanisms is found at the cell level, and could roughly be defined as such:

- Tropism is usually a growth movement due to uneven cell multiplication, which eventually leads to the organ orientation. A tropism is affected by a stimulus and its position. It can be positive (movement towards the stimulus) or negative (movement away from the stimulus).
- Nastic movement is usually a reversible movement due to hydraulic processes, e.g. change in cell turgescence. Such movement is always predefined by the motile structure and is thus independent of the direction of the stimulus (Boullard 1988; Gatin 1924; Jouy & de Foucault 2016).

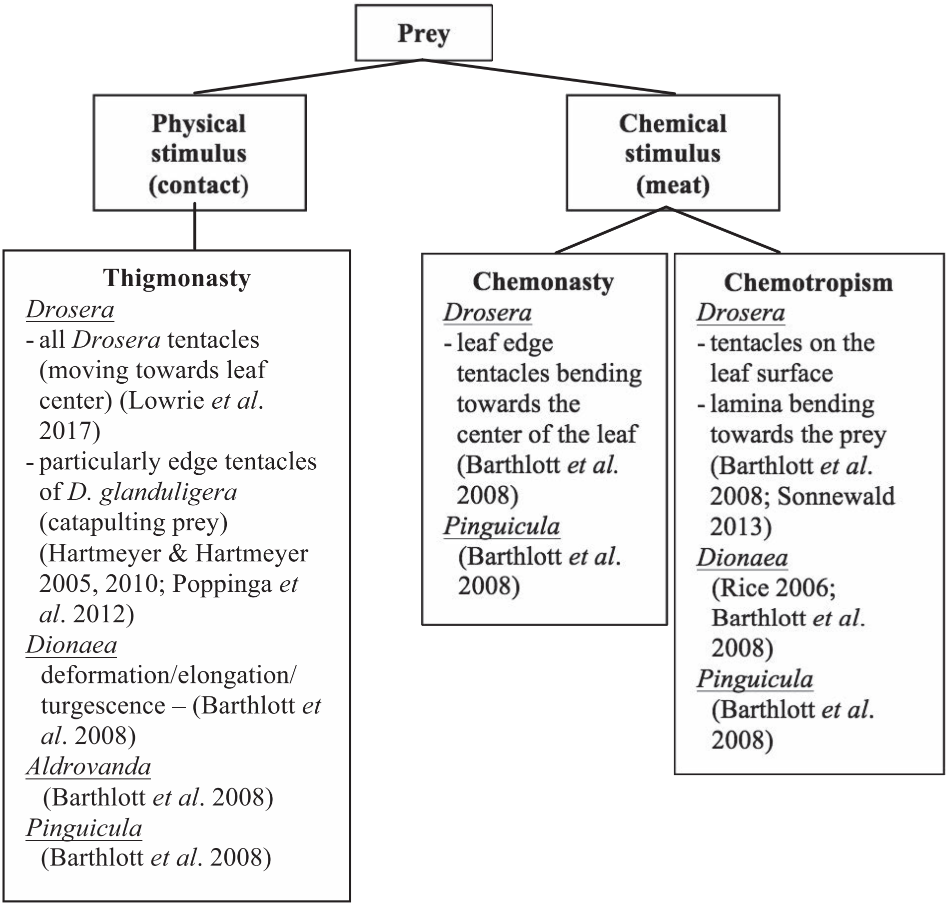
A same stimulus can induce those two kinds of movements. As quoted by Simón (2017), light stimulates phototropism. Plants kept on a windowsill will grow towards sunlight and this phenomenon is called positive phototropism. In addition, sunlight can also cause photonasty, i.e. nastic movement in response to a change in light intensity. For example, the alternation of opening and closing of flowers during day and night (e.g. *Mirabilis jalapa*, the four o'clock flower), or the bending of *Oxalis* leaflets at night.

When it comes to capture mechanisms associated with carnivorous plants, several movements are involved. Darwin (1875) himself established that the movement displayed by *Drosera rotundifolia* is due to two factors: contact and meat presence, or in other words, physical and chemical stimuli.

Contact stimulus induces thigmonasty

Some carnivorous plants exhibit active traps: prey are caught by quick movements, like *Dionaea* (Barthlott *et al*. 2008; Forterre *et al*. 2012), *Aldrovanda* (Cross 2012), and *Utricularia* (Tay-

Table 1. Summarized mechanisms in active and semi-active traps of carnivorous plants, with their associated stimuli (courtesy of V. Bazile).



lor 1989). It is also the case with some particular *Drosera* such as *D. glanduligera*, with external snap-tentacles catapulting visitors into the trap (Hartmeyer & Hartmeyer 2005, 2010; Poppinga *et al*. 2012). However, the origin of the trapping movement has often yet to be completely elucidated.

About the famous *Dionaea muscipula*, there is no consensus so far. Barthlott *et al*. (2008) suggested that it is a case of thigmonasty (nastic movement in response to contact) (Table 1). Specific cells, forming a sort of hinge, would undertake a vigorous turgor increase. This would result in their deformation and elongation, and ultimately in the trap closing. On the other hand, Legendre (2000) stated that a rapid multiplication of cells would be responsible for the snapping movement. Thus, the *Dionaea* trap does in no way perform a thigmotropism, although it is speculated that growth processes take place during trap lobe bending. The movement reaction (snapping) is always the same, independent to the direction of the triggering mechanical stimulus (S. Poppinga, pers. comm.).

As for *D. glanduligera*, Hartmeyer & Hartmeyer (2010) showed that upon stimulation, tentacles of *D. glanduligera* curve toward the lamina center and not toward the place where the stimulus occurred. Thus, this rapid catapult movement would clearly be a case of thigmonasty. In a less spectacular fashion, thigmonasty is generally observed throughout the genus *Drosera*, with a first, slow movement of all types of stalked glands (Lowrie *et al*. 2017). Similar observations were made with *Pinguicula*: when stimulated by inorganic matter, the leaf margins slightly curve by thigmonasty, then recover quickly (Lloyd 1942).

Chemical stimulus induces chemonasty and chemotropism

Besides contact stimulus, *Drosera* leaves react to the presence of certain molecules (Darwin 1875), notably NH_4^+ ions (Sonnewald 2013). Such chemical excitation causes a slow movement of both adjacent tentacles and the whole lamina (Darwin 1875; Barthlott *et al*. 2008). Contrary to what Simón (2017) suggested, this phenomenon is a two-fold mechanism (Table 1).

The first mechanism is based upon a chemically-induced nastic movement (chemonasty). The "*edge tentacles of the leaf are dorsiventrally structured and react chemonastically*" as stated by Sonnewald (2013). These tentacles do react to meat compounds, but the mechanism itself is not determined by the position of those compounds. All the tentacles of the leaf lamina edge bend towards the center by rapid cell expansion regardless of the prey position (Lowrie *et al*. 2017).

The second mechanism does involve tropism but since it is a chemical stimulus, the accurate name is chemotropism and should consequently be used. As every carnivorous plant enthusiast might have observed, for example in *Drosera capensis*, a trapped prey is surrounded by both tentacles and the leaf lamina. In this case, the movement is driven by the position of the stimulus, as the leaf and tentacles bend precisely towards the prey. Furthermore, this movement is due to cell growth (Lowrie *et al*. 2017), induced by increased growth hormone production (Barthlott *et al*. 2008) and can thus be considered as a tropism. According to Lloyd (1942), this mechanism was first observed by Batalin (1877) and later more explored by Hooker (1916, 1917). Tentacles bend towards the prey, stimulated by NH_4^+ ions among others (Sonnewald 2013).

Likewise, the sole presence of dead prey on a *Pinguicula* leaf induces movements. First, a chemonastic reaction takes place as the lamina surface becomes slightly concave due to a change of turgescence. It eventually forms like a small tray filled with leaf exudates (Barthlott *et al*. 2008; Rice 2006). Then, a chemotropic reaction follows as leaf margins bend towards the nutrient source, leading to the wrapping of the prey. Although this movement is very easily confused with the thigmonastic reaction triggered by contact stimulus, like Darwin did (1875), Lloyd (1942) showed that this wrapping movement is actually attributable to growth.

Finally, in *Dionaea muscipula*, after the trap closing due to thigmonasty, presence of organic compounds (such as ammonium, sodium, uric acid, coprostanol) entails a more complete closing by chemotropism (Barthlott *et al*. 2008). Both lamina lobes slowly approach each other, then shut the trap hermetically (Bailey & McPherson 2012). Here again, cell growth causes the movement (Rice 2006).

Conclusion

1. Leaf and tentacle movements in *Drosera, Pinguicula*, and *Dionaea* are due to several mechanisms.
2. The discussed mechanisms have had a name for a long time: thigmonasty, chemonasty, and chemotropism.

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