ZERO WATER FLOWS IN THE CARNIVOROUS GENUS GENUS GENLISEA

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In carnivorous plants, researchers seek to elucidate unique processes such as enzyme secretion, nutrient absorption from prey, rapid trap movements, and the ecological importance of carnivory. Among these processes, one of the most mysterious is water flow in *Utricularia* (bladderwort) traps. These 1-4 mm long, bladdershaped suction traps pump out water to maintain internal underpressure (Juniper *et al.*, 1989). After irritation by prey, the trap is quickly opened and the prey is sucked into the trap. No lesser mystery is the functioning of *Genlisea* traps (Juniper *et al.*, 1989; Meyers-Rice, 1994; Studnicka, 1996; Barthlott *et al.*, 1998). *Genlisea* species—wetland or amphibious plants from South America and tropical Africa are closely related to *Utricularia* (Lentibulariaceae).

Genlisea forms short stems with a rosette of small photosynthetic, green leaves and subterranean white traps. These traps are highly modified carnivorous leaves without chloroplasts (see Figure 1; also Juniper *et al.*, 1989; Studnicka, 1996; Barthlott *et al.*, 1998). The inverted Y-shaped traps are 2-15 cm long and about 1 mm thick. The hollow arms of the trap open into the hollow tubular neck (inner diameter 200-500 micrometers), which ends in a slightly dilated vesicular cavity. The whole central cavity of the arms and neck is filled with water and is lined with detentive hairs pointing towards the vesicle. As such, *Genlisea* traps function as "eel traps." Thus, microscopic prey are attracted to enter the traps and, thanks to the hairs, are led forward to the vesicle. Here, enzymes are secreted, and the prey is digested. It has been found recently that the traps of *Genlisea* are specialized for attracting and catching protozoa (Barthlott *et al.*, 1998). However, besides living or decomposed prey (Barthlott *et al.*, 1998) and sometimes also algae (Studnicka, 1996), fine soil particles have often been found in the vesicles (Juniper *et al.*, 1989; Meyers-Rice, 1994; Studnicka, 1996).

Based on this finding, on overall similarity to traps of *Utricularia*, and on considerations of the absorption efficiency of the traps, a hypothesis of active water flow in *Genlisea* traps exists (Juniper *et al.*, 1989; Meyers-Rice, 1994) with a supporting mathematical model (Meyers-Rice, 1994). Assuming the same water flow rate in *Genlisea* traps per trap wall unit area as in *Utricularia* traps during the resetting phase, a water flow rate of 14 micrometers per second in the neck cavity towards the vesicle was calculated. This rate exceeded by about three-fold a calculated rate of counter-diffusion of phosphate molecules (4.8 micrometers per second) at which phosphate, as a typical product of digestion of prey, could diffuse back from the vesicle and be lost from the trap. If this were so, the active permanent water flow would drag suspended soil particles and, to some extent, also living prey to the vesicle and prevent nutrients released in the vesicle from escaping due to diffusion (Meyers-Rice, 1994).

To test this hypothesis, I measured water flow in large traps of *G. violacea* (a "giant form" in horticulture) and *G. hispidula*. The plants were grown in a pot in a mixture of filamentous peat and perlite in a naturally lit greenhouse. Water flow through the traps was measured using a capillary glass microvolumeter (Dainty & Ginzburg, 1964) with a resolution of approximately 0.05 microliters and stability

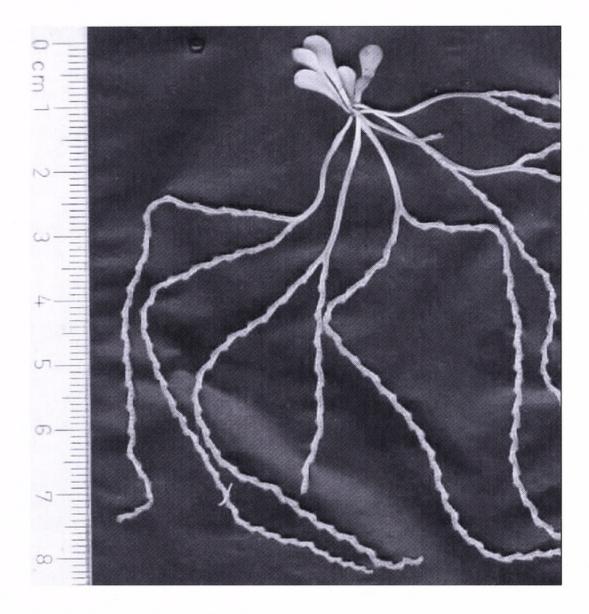


Figure 1: *Genlisea violacea* plants with green leaves and apoplastic white traps. The upper dilated part of the neck is the vesicle.

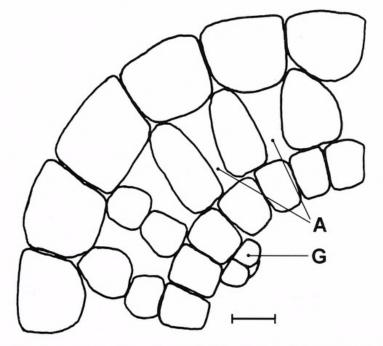


Figure 2: Schematized cross-section through *Genlisea violacea* vesicle. A: air spaces; G: sessile gland. The bar represents 50 micrometers.

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better than 0.03 nl s⁻¹. The expected water flow could range within approximately 0.17-3 nl s⁻¹ (Meyers-Rice, 1994). Traps of experimental plants were carefully released from the substrate and washed using tap water. A trap with shortened arms and without leaves was fixed using silicon cement in the neck of this device just above the bifurcation of the trap. After temperature stabilization in a thermostatted bath $(22.0\pm0.02^{\circ}C)$ in darkness, water flow was measured for 40-60 min.

Counter to the model, virtually zero water flow was measured in both species (n=8-10 in each species). These measurements prove that Genlisea traps are passive. The soil particles often observed in the vesicles could enter by another route, e.g. if pushed by captured prey (Studnicka, 1996). In light of these negative experimental results and the anatomy of the vesicles (see Figure 2), it is possible to offer several other arguments against the hypothesis of active water flow in Genlisea traps. Genlisea traps lack bifid glands which would be responsible for water pumping as in Utricularia (Juniper et al., 1989; Studnicka, 1996). The wall in Genlisea vesicles consists of 3-4 layers of large cells with voluminous air spaces, unlike the mere two layers of cells, without air spaces, in Utricularia traps (Juniper et al. 1989). The presence of large cells and voluminous air spaces would slow down any osmotically driven water flow. Utricularia traps pump water for only 20 minutes until the traps are ready to fire (Juniper et al., 1989; Meyers-Rice, 1994). The always-open Genlisea traps would have to pump water constantly to prevent loss of nutrients. Accordingly, such an operation would demand a large amount of energy, and the energetic cost would probably exceed the nutritional benefit. However, Genlisea traps might efficiently use mineral and organic nutrients released from prey in the vesicle, even without pumping water, if the rate of absorption of these nutrients in the vesicle and neck is sufficiently high. Merely a high density of absorptive sessile glands in the vesicle and along the neck could give evidence for this hypothesis.

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