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Aerodynamic trapping effect and its implications for capture of flying insects by carnivorous pitcher plants

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ABSTRACT

This experimental study tests the hypothesis that carnivorous pitcher plants may have developed passive aerodynamic means to trap a flying prey. Using a miniature propeller, it is shown that hovering inside a pitcher-like container induces a re-circulating flow that pulls the propeller down, towards the bottom, and that the magnitude of this effect depends on the shape of the container and the location of the propeller. Analogously, re-circulating flow induced by a hovering insect inside the trap of a carnivorous pitcher plant should pull it towards the bottom of the trap, possibly preventing its escape.

1. Introduction

Carnivorous pitchers evolved separately in various plant families, in particular in the Nepenthaceae, the Sarraceniaceae and the Cephalotaceae [1,2]. In all these families, leaves or leaf parts develop as vertical containers, capable of trapping (and digesting) various organisms, mostly insects. The prey provides nutrients in habitats where soil minerals are less available [3].

The prey is lured to the traps by olfactory cues [4] and by specific color patterns [5,6] that exploit the spontaneous perceptual biases that guide insects in their search for food [7]. In most species the visiting insects are rewarded with nutritious nectar [8,9] that is secreted at the internal collar-like ridge that lines the pitcher rim (the peristome), and at this very place some of the visiting insects lose foothold and fall down into the pitcher cavity [8,10].

The majority of studies on the trapping mechanism in pitcher plants took for granted that once an insect loses its foothold at the peristome, it would fall all the way down into the digestive liquid at the bottom of the trap. But why would a flight-capable insect not take off immediately when losing its foothold and fly out of the trap? Insects can initiate flying within a few hundredths of a second from being triggered [11], leaving, in principle, enough time to escape the digestive liquid at the pitcher bottom. In this study we examine the hypothesis [1, p. 108] that the architecture of some of the pitcher traps induces passive *aerodynamic trapping* of certain flying insects within the cavity of the trap. In other words, even if these insects start flying, they may not be able to escape their doom.

2. Aerodynamic considerations

In order to hover, a vehicle (we shall use this term for animals and mechanical machines alike) has to produce thrust that equals its weight. Since the thrust is produced through interaction between the vehicle and the fluid (air) that surrounds it, the thrust acts to increase the momentum and the energy of the fluid, creating a downward flowing jet (Fig. 1(a)). If we assume, for the sake of argument, that the fluid is inviscid, the rate at which the energy is supplied to the fluid, P_i, equals the product of thrust, T, and velocity of the jet where the thrust is produced, v_i:

$$P_i = T v_i. \quad (1)$$

P_i is commonly referred to as the induced power [12].

Since the velocity of the thrust-producing parts (wings of an insect or blades of a rotor) during hovering is invariably large as compared with v_i, the time-averaged thrust production (over a few cycles) can often be approximated using the actuator disc concept. In a nutshell, the idea is to associate the time-averaged thrust with an equivalent pressure jump across an infinitesimally thin

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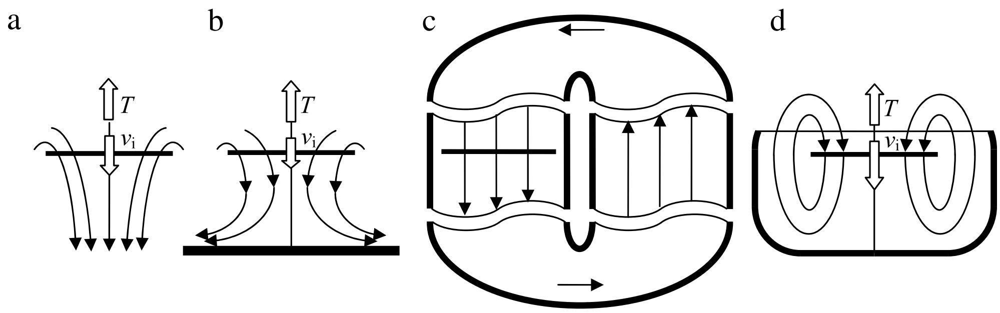

Fig. 1. Schematic stream lines of the flow induced by an actuator disc: (a) with no boundaries; (b) in ground effect; (c) inside a closed tube; (d) inside a trap (hypothesized). The disc is marked by a thick horizontal segment; in all cases the thrust is directed upward.

sector (disc) swept by the wings during their motion cycle [13]. When the domain of fluid in which the thrust is produced is unbounded (Fig. 1(a)), the (effective) axial velocity through the thrust-producing disc, which we can now associate with v_i, immediately follows by momentum considerations. They furnish

$$v_i = \sqrt{T/(2k_i\rho A)}, \tag{2}$$

where ρ is the density of the fluid, A is the disc area and k_i is a certain numerical factor depending on how the equivalent pressure jump is distributed across the disc; it equals unity when this distribution is uniform [14].

When the domain of the fluid is bounded – as, for example, by walls of a trap or by the ground – Eq. (2) can no longer be derived from simple momentum considerations, but it remains correct from dimensional considerations. In this case k_i becomes a phenomenological constant reflecting not only the pressure jump distribution across the thrust-producing disc, but also the geometry of the domain boundaries. For example, when the disc is lowered toward the ground in otherwise unbounded fluid, k_i increases, and hence v_i decreases (Fig. 1(b)); the associated power reduction is widely exploited in helicopters' operations [14].

Let us consider now an idealized helicopter attempting to hover in the midst of a vertical tube, neatly enclosing the rotor disc. As long as both ends of the tube are open, it should have no principal difficulty to do so. Now, take the end of the tube below the rotor, bend it into a doughnut, and plug it into the end of the tube above the rotor, trapping both the fluid and the rotor inside (Fig. 1(c)). In this case, all the fluid ejected down by the rotor returns to it from above. Recall that the fluid is still considered inviscid, and that a hovering rotor constantly pumps energy into the fluid at the rate given by Eq. (1). Since the mass of fluid in motion is now limited to that trapped inside the tube, this constantly supplied energy will make the fluid to accelerate. Since for a given thrust, increasing v_i implies increasing P_i (Eq. (1)), the power required to hover will eventually turn infinite. To put it simply, a helicopter – or, to the same end, a flying insect – with limited power cannot hover in a closed tube filled with an inviscid fluid. In a different form, comparable arguments can be found in Ref. [15].

By analogy with this imaginary experiment, we infer that if the walls of a pitcher trap divert the fluid jet induced by a hovering insect so as to be sucked back, v_i will increase, and so will the power required to remain in hover (Fig. 1(d)). If the insect does not have this extra power, it is doomed. This is the passive *aerodynamic trapping* phenomenon mentioned in the Introduction.

3. The approach

We lack the tools to solve the problem of the aerodynamic trapping analytically, but we intend to prove its existence experimentally. To this end we do not need a real plant and we do not need a real insect. Exploiting the actuator disc analogy [13], it suffices to demonstrate that there exists a container (pitcher) that reduces k_i for some type of hovering vehicle.

The idea is the following. Take a miniature fixed-pitch propeller – which is as good an actuator disc as an insect – and connect it to a small electrical motor at the tip of a long probe. Suppose that it is possible to accurately position the tip of the probe and to measure both the electrical power P_e supplied to the motor (through voltage and current) and the tip velocity v_t of the blades (through rpm). It is shown in Appendix A that the power coefficient $C_P = P/(\rho v_t^3 A)$ needed to rotate the propeller can be approximated by

$$C_P = C_{P,0} + 2C_{P,1}C_{T,2}^3 B^2 f(8k_i B), \tag{3}$$

where,

$$B = \beta C_{T,1}/C_{T,2}^2; \tag{4}$$

β is the representative pitch angle of the blades; $C_{P,0}$, $C_{P,1}$, $C_{T,1}$ and $C_{T,2}$ are (unknown) coefficients depending mainly on the propeller geometry, and weakly on its operating conditions; whereas

$$f(x) = \left(-1 + \sqrt{1+x}\right)^3 / x^2. \tag{5}$$

f is monotonically increasing over $(0, 8)$ and monotonically decreasing over $(8, \infty)$ (we tacitly assume that $k_i B > 0$), but since we do not actually know the coefficients in (3), we do not know *a priori* if $f(8k_i B)$ increases or decreases with k_i.

As the first step, we place the propeller far from any boundary, measure the input power and rpm, and compute the respective power coefficient $C_{P,e} = P_e/\left(\rho v_t^3 A\right)$. This coefficient should be equivalent to C_P – the ratio between the two is the electro-mechanical efficiency of the motor. Next, we place the propeller close to a flat boundary, mimicking a helicopter hovering in ground effect. We repeat the measurements and find $C'_{P,e}$. Since we know *a priori* that in ground effect $k'_i > k_i$ [14], obtaining $C'_{P,e} > C_{P,e}$ implies that f is an increasing function of its argument (and therefore $Bk_i < 1$). Of course, if $C'_{P,e} < C_{P,e}$, the opposite is true (and therefore $Bk_i > 1$). As the last step, we take a pitcher-like container – and it can be an ordinary glass of suitable dimensions – and place the propeller in its interior. Repeating the measurements we obtain $C''_{P,e}$. If $C'_{P,e} > C_{P,e} > C''_{P,e}$ or $C'_{P,e} < C_{P,e} < C''_{P,e}$, then $k'_i > k_i > k''_i$, and the aerodynamic trapping concept can be considered proved.

There are five tacit assumptions underlying the preceding arguments. One is that the electro-mechanical efficiency of the motor does not change appreciably throughout the test. The other four are that the coefficients $C_{T,1}$, $C_{T,2}$, $C_{P,1}$ and $C_{P,0}$ in Eqs. (3) and (4) do not change appreciably with the introduction of boundaries – or, which is equivalent, with small variations in rotor speed or with small variations in the induced velocity distribution across the rotor disc.

The first assumption will be verified experimentally by demonstrating that with no boundaries $C_{P,e}$ is independent of the rotor speed (see Step 1 below) and independent of time (see Step 2 below). The following three assumptions are assessed in