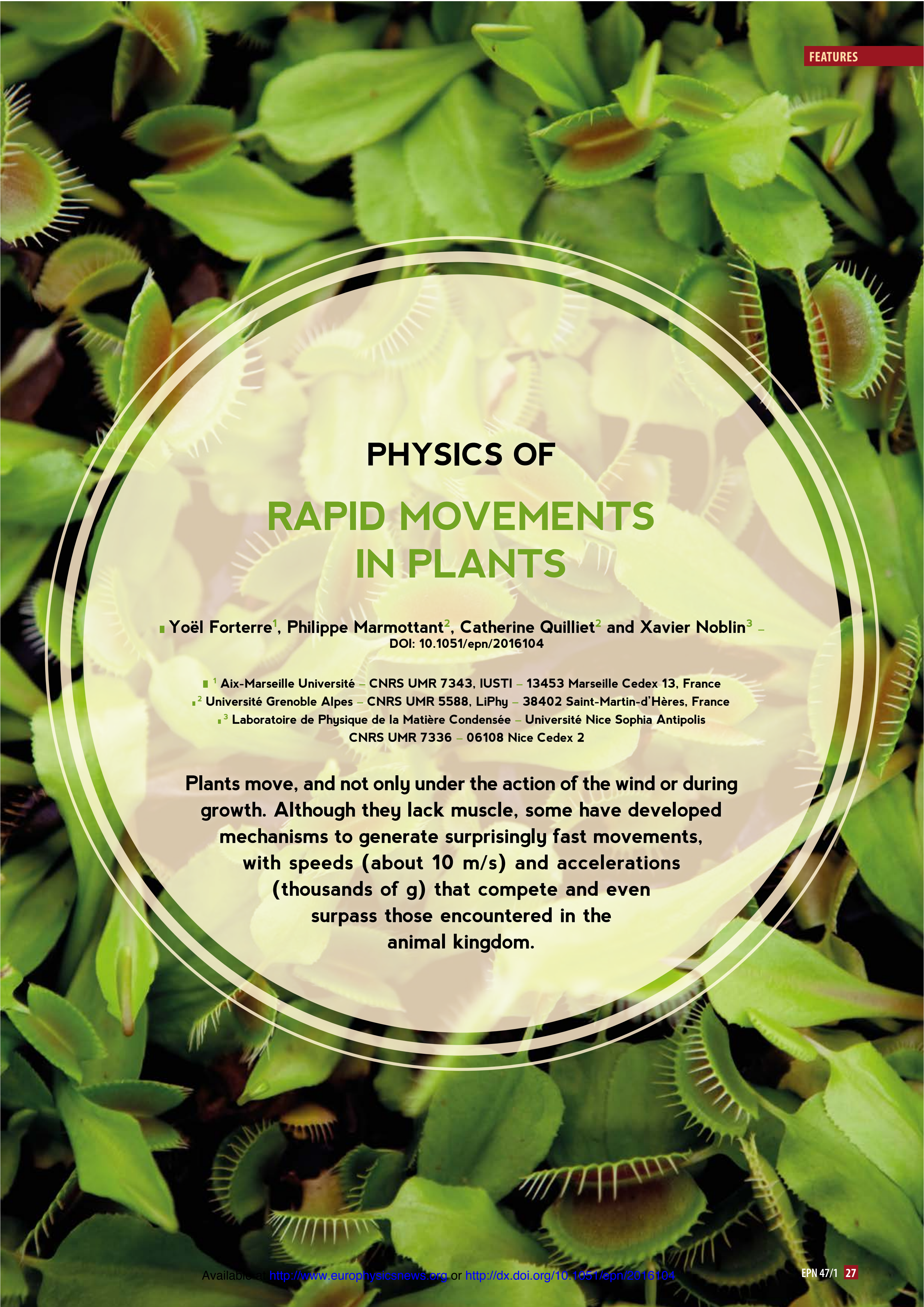

PHYSICS OF RAPID MOVEMENTS IN PLANTS

Yoël Forterre[1], Philippe Marmottant[2], Catherine Quilliet[2] and Xavier Noblin[3] –

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[1] Aix-Marseille Université – CNRS UMR 7343, IUSTI – 13453 Marseille Cedex 13, France
[2] Université Grenoble Alpes – CNRS UMR 5588, LiPhy – 38402 Saint-Martin-d'Hères, France
[3] Laboratoire de Physique de la Matière Condensée – Université Nice Sophia Antipolis
CNRS UMR 7336 – 06108 Nice Cedex 2

Plants move, and not only under the action of the wind or during growth. Although they lack muscle, some have developed mechanisms to generate surprisingly fast movements, with speeds (about 10 m/s) and accelerations (thousands of g) that compete and even surpass those encountered in the animal kingdom.

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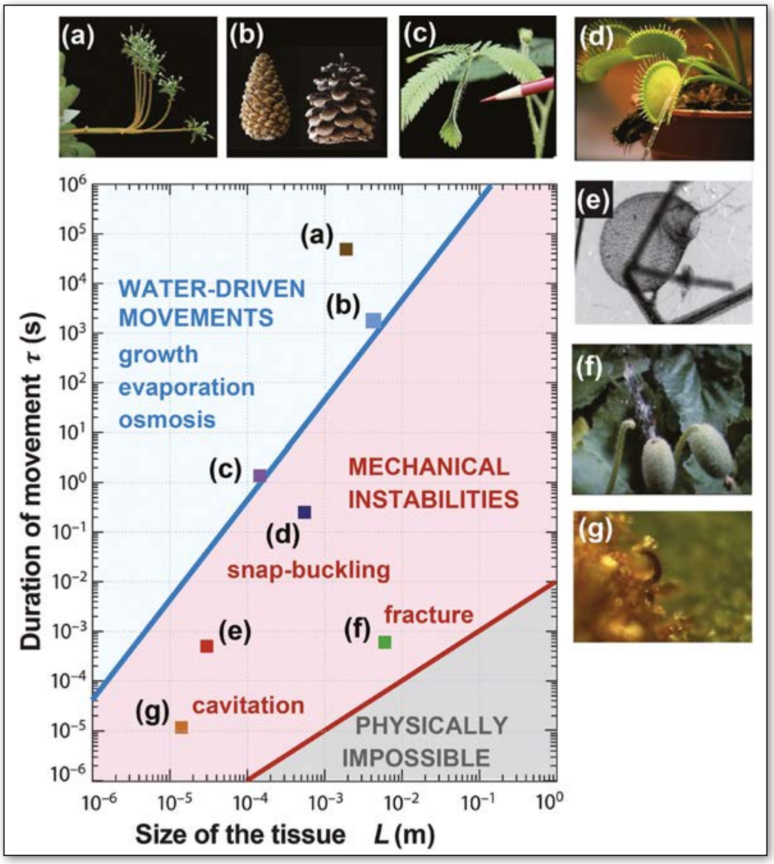
These fast movements are used to fulfill important functions such as reproduction (pollen catapult in some Orchids, explosive dispersal of seeds), defense against predators (the folding of the *Mimosa pudica* leaves) or nutrition (the traps of carnivorous plants). They have fascinated scientists since the first observations by Darwin and Linné and raise important questions in biology related to water transport across the cellular membrane, the mechanics of the cell wall or the perception of mechanical signals by plants. In this article, we discuss the physical mechanisms developed by plants to generate these rapid movements, in the light of recent studies carried at the frontiers of physics and biology.

Water-driven movements: turgor pressure, osmosis and evaporation

First of all, a crucial point in order to understand what a plant can do and cannot do is that, contrary to animal cells, plant cells are glued together and surrounded by a rigid cell wall mainly made of cellulose [1]. This prevents plant cells from using soft contractile proteins like those in animal muscles to deform and generate movement. However, the stiff wall allows plant cells to sustain a very high internal water pressure ("turgor pressure"), typically 4-8 bars and possibly up to 40 bars in special cells. Water in plants may also undergo negative pressures, thanks to the cohesive forces between water molecules, resulting in an inward pulling on walls; the mature cell wall of woody plants avoids damaging of structure even at the highest negative pressures (~ -100 bars).

Physically, such high absolute values of the hydrostatic pressure results from osmosis or evaporation phenomena [2,3]. The water fluxes between the plant and its surrounding induce a swelling or shrinking of the plant cells. This causes an internal turgor pressure, which in turn induces a mechanical movement at the macroscopic scale. Some of these movements correspond to an irreversible deformation of the cell walls, such as growth and the oriented movements against light or gravity (Fig. 1a). Some other are associated to a reversible motion, such as the osmotically induced folding of the sensitive leaves of *Mimosa Pudica* (Fig. 1c), or the opening/closing of pine cones depending on hygrometry (Fig. 1b).

▼ FIG. 1: Physical classification of plant movements according to the duration of the movement τ and the typical size L of the tissue over which motion occurs (adapted from[4]). Border $\tau = \tau_p$ (blue line) gives the poroelastic time (*i.e.*, the quickest movement based on water transport only), calculated using as diffusion coefficient of water in plant tissue the average value $D \sim 10^{-8}\ m^2/s$. Border $\tau = \tau_i$ (red line) gives the inertial time (*i.e.*, the quickest possible movement set by inertia and elasticity), obtained using as density $\rho = 1000\ kg/m^3$ and as Young modulus the typical value $E = 10$ MPa. (a) Growth response to gravity. (b) Hygroscopic motion of pine cone scales. (c) Folding back of *Mimosa Pudica* through osmosis. (d) Carnivorous plant Venus flytrap. (e) Carnivorous plant *Utricularia*. (f) Propulsion of seeds of *Ecballium elaterium* ("squirting cucumber"). (g) Catapult movement of a fern sporangium.



Physical limit on the speed of water-driven movements: the poroelastic timescale

For motions uniquely powered by water exchange, the speed is limited by the timescale for water transportation through the tissue [4]. In a porous and elastic medium like the plant tissue, this latter is a diffusive process that operates on a time $\tau_p = L/D$, where L is the transportation distance, and D an effective diffusion coefficient that takes into account the elastic and hydraulic properties of the medium. This time τ_p, called "poroelastic time", is compared in figure 1 to the duration τ of various motions observed in the vegetal kingdom, versus the typical size L of the moving tissue. Indeed, the duration of motions associated with growth (Fig. 1a) or due to modifications of ambient moisture (Fig. 1b) are to be found above the boundary $\tau = \tau_p$, which is consistent with their purely "hydraulic" nature. The rapid folding of Mimosa Pudica leaves also falls under this regime, even if, due to the small distances over which water has to be carried, the typical time of the motion is impressively short (typically 1 s).

Speeding up plant movements: elasticity and mechanical instabilities

If plants were relying only on water transport to move, they could not generate movements on a timescale shorter than the poroelastic time. However, figure 1 shows that many plants have managed to cross this hydrodynamic limit. Their common strategy is to take advantage of a mechanical instability, *i.e.*, a rapid release of previously stored energy when a threshold is crossed. Two types of instabilities are used by plants to generate fast movements:

(i) snap-buckling instabilities for the traps of carnivorous plants such as the Venus flytrap or the bladderworts, and (ii) ruptures, either solid or liquid (cavitation), for propulsion of seeds or spores. In the following, we discuss these two classes of mechanisms.

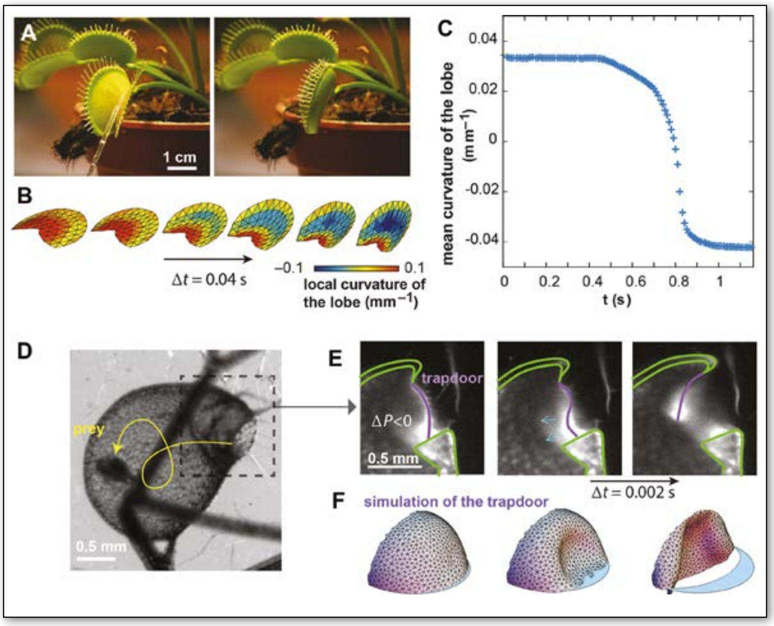
Snap-buckling instabilities: carnivorous plants Venus flytrap and Utricularia

The trap of the carnivorous plant Venus flytrap (*Dionaea muscipula*) – called by Darwin the « Wonder of Nature » – is composed of two lobes attached by their base, that form a jaw (Fig. 2A). The internal side of each lobe contains mechano-sensitive hairs, which generate an electrical signal when touched. The trap closes in a few tenths of a second, which is too rapid to be due only to water transportation (Fig. 1). Recent studies have shown that the mechanism that amplifies the speed of closure relies on snap-buckling instability, analogous to the buckling of an elastic shell [5,6]. The two lobes of the trap are curved outward in the open state and inward in the closed state (Fig. 2B,C). Upon triggering, the lobes actively change their natural curvature, *i.e.*, the lobes 'try' to bend inward. However, because of the geometrical constraint of the shell-shape lobe, this active bending causes the trap to accumulate elastic energy, until the stored energy becomes so large that each lobe buckles inside out, rapidly snapping the trap shut.

A similar mechanism has been shown to operate in the suction trap of the less known but ubiquitous bladderworts (*Utricularia*) [7]. Each trap of this aquatic plant is remarkably sophisticated. It is made of an elastic closed leaf, bladder-shaped, in which water pressure slowly decreases under the action of pumping glands (Fig. 2d). The sealing of the trap is ensured by a flexible door that holds a few long sensitive hairs. Suction occurs within one millisecond – a record – thanks to an instability mechanism that, here too, results from a snap-buckling instability. In the initial configuration, the trapdoor is a shallow dome whose convex face is facing outward, thereby resisting the pressure difference across it much like a Gothic vault in architecture. Triggering lowers this resistance, either through an electrical signal or just as a weakness point, which induces a buckling of the door and its rapid opening (Fig. 2E,F). Surrounding water is then quickly sucked in, with an acceleration of up to 600g, and it drags small preys that cannot swim against such a flow (Fig. 2D).

Cavitation instability: propulsion of fern spores

Rapid movements may also be required for the dissemination of reproductive materials (seeds, pollens, spores). The squirting cucumber (Fig. 1f) is well known by the impressive way it launches its seeds, but the more discrete catapulting of spores ferns (Fig. 3A) is probably the most elegant mechanism. In most species of ferns, spores are gathered in quasi-spherical capsules (the “sporangia”) holding a ring-like ridge that consists of a dozen of water-filled cells (the “annulus”) (Fig. 3B). Evaporation of water from these cells induces a negative water pressure that pulls the cell walls in. Since the walls are thinner on the external side, they can bend inwards. This induces a slow and global outwards curvature at the ridge scale, up to the point (negative pressure around -100 bars) where cavitation bubbles catastrophically appear in the cells and grow, abruptly relaxing the stored elastic energy into a rapid closure of the sporangium, and ejection of its spores like in a catapult.



▲ **FIG. 2:** Snap-buckling instability in carnivorous plants *Venus flytrap* (a-c) and *Utricularia* (d-f). **(A)** Venus flytrap in the open **(left panel)** and closed **(right panel)** state. **(B)** Three-dimensional shape reconstruction of the lobe of one trap during closure (experiment, Δt is the time interval between two successive images). **(C)** Spatially averaged mean curvature of the lobe vs. time; the trap was triggered at $t = 0$. **(D)** *Utricularia* trap and trajectory of a small soft water crustacean, sucked in just after door opening. **(E)** Inversion of the trapdoor and buckling of the median door axis visualized by light sheet fluorescence microscopy. **(F)** Numerical simulation of the trapdoor opening. **(figures A-C according to [5] ; figures D-F according to [7])**

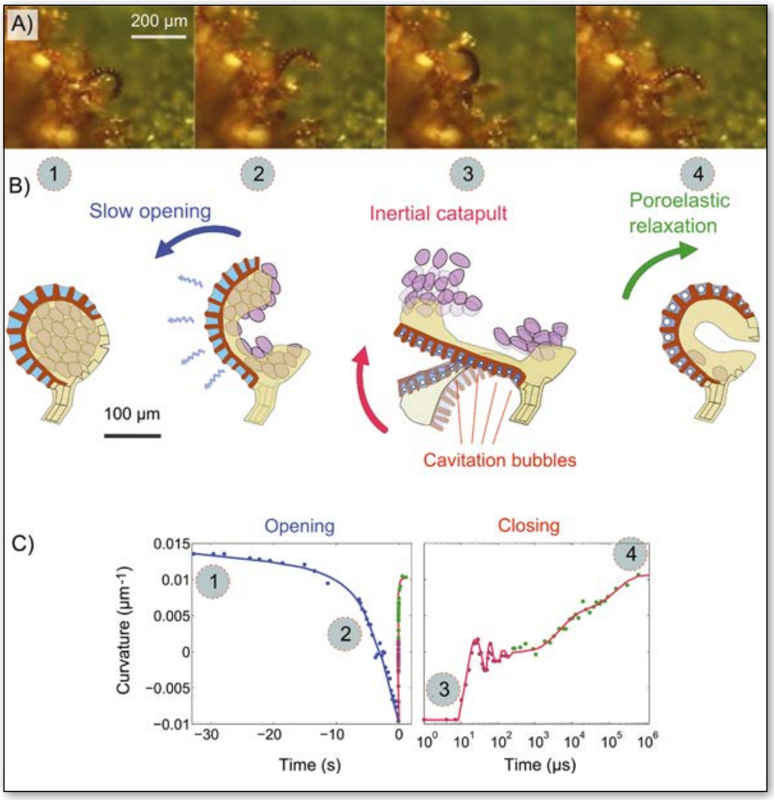
The ejection mechanism was roughly understood for more than one century, but many questions were not addressed until recently. In particular: how can the sporangium so efficiently propel its spores in the absence of any end-stop? In medieval or roman catapults, end-stops were used to arrest the catapult arm at half course, having it eject its projectile before it was tackled back on the floor. Recent experiments using ultrafast cameras have unveiled for the first time the ejection dynamics and explained how the sporangium functions without any structural end-stop [8]. The dynamics actually exhibits two phases occurring at very different timescale (Fig. 3C). The first one occurs just after cavitation and consists of the partial closure of the ring in a few tens of microseconds (probably the swiftest movement in the vegetal world), due to the transformation of the stored elastic energy in the sporangium annulus into kinetic energy. This inertial phase is so quick that the water trapped in the porous walls of the ridge has not yet been redistributed. Hence, water pressure suddenly increases during the motion, which transiently stops the ridge at half course, and allows spores ejection at more than 10 m/s. In a second phase, after relaxation of the inertial oscillations of the annulus, water pressure slowly relaxes and the sporangium completely closes within a few hundreds of milliseconds. It is impressive to see how such a small system made of water and a few cells can perform all the key functions of a catapult, from the motive force for charging the catapult (water cohesion and evaporation) to triggering (cavitation), followed by end-stop due to the poroelastic behaviour of the cell walls.

Conclusion

Plants are hydraulic machines and most of their movements are simply the consequence of water flow driven by osmosis and evaporation phenomena. They are thus limited in speed by the poroelastic timescale of water diffusion through the soft plant tissue. In this article, we have seen how plants can use mechanical instabilities, such as elastic buckling, fracture or cavitation, to suddenly release some stored elastic energy and speed up their movements beyond the poroelastic limit. These elastic movements are nevertheless ultimately limited by the inertial time needed to accelerate masses [4]. This latter is set by the speed of the elastic waves in the body, and given by the inertial-elastic time $\tau_i = L/c$, where L is the object size and $c=(E/\rho)^{1/2}$ the speed of elastic waves, where E is the material Young modulus and ρ the material density. No plant movements are found below this limit (Fig. 1).

Fast plants are not only wonders for curiosity cabinets. Together with an increasing occurrence of biomimetic breakthroughs, they are a promising source of inspiration for realizing artificial micro-systems, such as micro-fluidic actuators [10], fast responsive surfaces [11] or jumping robots [12]. ■

▼ **FIG. 3: (A)** Opening and closing of a fern sporangium (which has already launched its spores). **(B)** Ejection mechanism in 4 steps, corresponding to the 4 pictures in (A) (on the third image in A), onlyposition before the triggering is displayed). **(C)** Mean curvature of the sporangium vs. time for the slow opening (blue curve) and the rapid closing (red curve). The logarithmic scale helps to separate the short time inertial oscillations of the first phase and the long time poroelastic relaxation of the second phase (according to [8]).



About the Authors

Yoël Forterre is CNRS researcher at IUSTI, Aix-Marseille University. He is working on granular materials, complex fluids, and plant biophysics (Venus flytrap mechanism of closure, plants response to gravity, hydraulic signals in relation with plants mechano-perception).

Philippe Marmottant is CNRS researcher at LIPhy Grenoble, and is interested in the physics of plants, including bladderworts suction traps, horsetail spores and sap flows in trees.

Catherine Quilliet is academic at Grenoble University. At LIPhy, she has opened for a few years her soft matter research themes to the deformations of elastic surfaces, in the aim to link the shape of soft objects to their small-scale properties.

Xavier Noblin is CNRS researcher at LPMC, Nice, working on soft matter (wetting, bubbles, microfluidics, granular media), biophysics (plant and fungi mechanics) and biomimetics.

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