

The Fern Sporangium: A Unique Catapult

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Spore dispersal in plants and fungi plays a critical role in the survival of species and is thus under strong selective pressure. As a result, various plant and fungal groups have evolved ingenious mechanisms to disperse their spores effectively (1, 2). Many of these mechanisms use the same physical principles as man-made devices but often achieve better performance. One such dispersal mechanism is the cavitation-triggered catapult of fern sporangia. The sporangia open when dehydrating and use the stored elastic energy to power a fast closure motion that ultimately ejects the spores. The beauty of this dispersal mechanism and its similarity with medieval catapults have not escaped notice (1). All man-made catapults are equipped with a crossbar to stop the motion of the arm midway. Without it, catapults would launch their projectiles into the ground. This crossbar is conspicuously missing from the sporangium, suggesting that it should simply speed up to its closed conformation without ejecting the spores. We show that much of the sophistication of this ejection mechanism and the basis for its efficiency lie in the two very different time scales

associated with the sporangium closure. The simple structure of the sporangium belies the complexity of its action (Fig. 1A). Central to the ejection process is the annulus: a row of 12 to 13 cells that forms a crest to one side of a spherical capsule enclosing the spores. As the annulus cells lose water by evaporation, water tension builds up within them, thus forcing the thickened radial walls closer together and causing lateral walls to collapse internally (3, 4) (Fig. 1B and movie S1). The whole annulus is thus bent out of shape, much like an accordion in the hands of a musician. The strong change in curvature (Fig. 1, B and D) forces the opening of the sporangium at the stomium, thus exposing the spores. When water tension in the annulus cells reaches a critical value [about -9 MPa (5)], cavitation occurs within adjacent cells (6) (Fig. 1C, fig. S2, and movies S2 and S3). The annulus then closes by 30 to 40% within about $10 \mu\text{s}$, leading to a quick release of the energy stored in the annulus and expulsion of the spores at an initial velocity of up to 10 m s^{-1} (7). This corresponds to an acceleration of about $10^5 g$. This first phase is followed by a comparatively

slow relaxation to an 85% closed configuration in a few hundreds of ms. We interpret the two time scales as a fast inertial recoil of the annulus followed by a slow poroelastic dissipation (8) of the energy remaining in the annulus. The annulus walls are constituted of a tight network of cellulose fibers surrounded by water that flows to conform to their relative displacements. The tiny size of the pores (9) and thick walls (10) induce strong viscous losses (from Darcy's law) that dramatically slow down the annulus motion. This dynamic can be described by using a generalized viscoelastic Maxwell model that fits our data very well and integrates all the physical forces at play (Fig. 1E and fig. S3). The measured and predicted time scales are in good agreement both for the inertial (respectively 25 and $27 \mu\text{s}$) and the poroelastic (respectively 5.8 and 3 ms) regimes. The coexistence of these two widely different time scales allows the sporangium to release its spores efficiently without the use of structural elements to arrest the recoil motion.

A dozen cells placed in a row can fulfill all the functions of a medieval catapult, including the motive force for charging the catapult (water cohesion), energy storage (annulus wall), triggering mechanism (cavitation), and returning motion arrest (poroelastic behavior of the annulus wall).

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Supporting Online Material

www.sciencemag.org/cgi/content/full/335/6074/1322/DC1

Materials and Methods

Fig. S1 to S4

References

Movies S1 to S4

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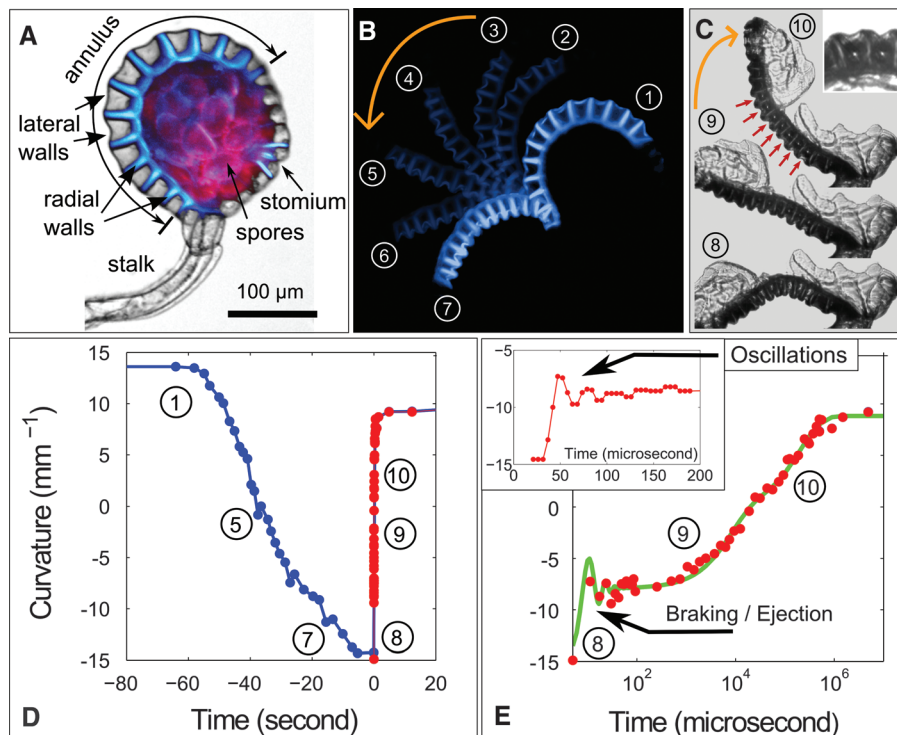


Fig. 1. (A) The sporangium of *Polypodium aureum*. Annulus geometry during sporangium opening in (B) and in (C) just before cavitation and 0.4 and 40 ms after cavitation. Note the seven cells that have cavitated (red arrows). (D) Annulus curvature during opening (blue) and closing (red) phases. (E) The closing phase in log-linear scale reveals the poroelastic relaxation; the green line represents the fit from our model. The numbers correspond to frames in (B) and (C). (Inset) Expanded view of the inertial oscillations.



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