

# Finessing the fracture energy barrier in ballistic seed dispersal

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**Fracture is a highly dissipative process in which much of the stored elastic energy is consumed in the creation of new surfaces. Surprisingly, many plants use fracture to launch their seeds despite its seemingly prohibitive energy cost. Here we use *Impatiens glandulifera* as model case to study the impact of fracture on a plant's throwing capacity. *I. glandulifera* launches its seeds with speeds up to 4 m/s using cracks to trigger an explosive release of stored elastic energy. We find that the seed pod is optimally designed to minimize the cost of fracture. These characteristics may account for its success at invading Europe and North America.**

biomechanics | fracture mechanics

**E**xplosive dehiscence is a common seed dispersal strategy in plants (1). The mechanism is analogous to a catapult (2): stored elastic energy is rapidly released and converted into kinetic energy of the seeds. Unlike in the catapult however, there is no equivalent in the plant kingdom of a mechanical latch to trigger the energy release and plants instead resort to physically breaking the bonds that sequester the elastic energy. For explosive dehiscence the bond breaking is accomplished by a fast moving crack. However, cracks consume energy and should thus significantly degrade the efficient use of stored energy. Here we investigate the energy balance in the fracture mediated seed dispersal of *Impatiens glandulifera* Royle, one of the most invasive nonnative plant species in Europe (3–5) and North America (6, 7). We find that the construction of the seed pod is a marvel of natural design that achieves a highly efficient energy transfer by exploiting the fleetness of fracture, finessing the fracture energy cost, and coordinating the simultaneous fracture of its five seams.

The seedpod of *I. glandulifera*, shown in Fig. 1A, consists of 5–10 seeds held within a shell comprised of five elongated segments or valves (8). The relaxed shape of a single valve is curled, as shown in Fig. 1B. When the seedpod is whole, the valves are held straight in a state of tension by a membrane connecting adjacent valves. Seed ejection proceeds as shown in Fig. 1D: a single seam cracks, minute contractions of the pod split the remaining seams (not visible in Fig. 1B), and now fully freed the valves contract and accelerate the payload.

During the ejection sequence, the mechanical energy stored in the valves in the form of elastic potential energy  $U_e$  is released. Some of this energy pays for the fracture energy  $U_f$ , some is transferred to the kinetic energy of the seeds  $K_s$  and valves  $K_v$ , and the remainder  $D$  is lost due to dissipative processes. From energy conservation  $U_e = U_f + K_s + K_v + D$ .

We measured the force needed to stretch a seed pod from a fully open state to a closed state (see e.g., Fig. 2) and calculated  $U_e$  from the area under the force-separation curve. We obtain a value  $U_e = 0.9 \pm 0.2$  mJ. We determined the kinetic energy  $K_s$  of the seeds using high speed video to measure the speed of the seeds. We ignore the rotational kinetic energy due to its smallness (see ref. 9). The mean mass of a seed  $m$  was measured to be 19.9 mg ( $N = 7$ ), the mean speed of the seeds  $u$  was measured to be  $3 \pm 1$  m/s ( $N = 4$ ). The kinetic energy of the seeds  $K_s = n \frac{1}{2} m u^2 = 0.62 \pm 0.2$  mJ, where  $n = 7$  is the mean number of seeds per pod. Kinetic energy imparted to the valves is difficult to quantify due to their odd shape and motion of the valves

(see Movie S1). An estimate based on the mass of the five valves (0.1 mg) and the speed of the seeds (because part of the valve must be moving at least as fast the seed) gives a value of 0.4 mJ. Thus, almost all the stored energy is converted into kinetic energy. Interestingly, similar measurements on *Impatiens capensis* show much lower conversion efficiency (9); we revisit this difference below.

Given that almost all the stored energy is transferred into kinetic energy, the fracture energy must be small. Estimating the fracture energy, however, leads to the opposite conclusion. We assume that the material is brittle (see ref. 2). The fracture energy is proportional to the new surface area created by a crack and a material dependent constant  $\Gamma$  with units of energy per unit area. The total fracture energy for the seed pod  $U_f = 5 \times 2\Gamma tL$  where  $t$  and  $L$  are the seam thickness and length; the factor for five corresponds to the number of seams. A conservative estimate for  $\Gamma$  is 10 J/m<sup>2</sup>, the fracture energy of wood along its grain (10) and to the best of our knowledge the lowest value for plant matter in the published literature. With  $L = 2.5$  cm and  $t = 300$   $\mu$ m from measurement, and thus  $U_f \approx 0.6$  mJ. Clearly something is wrong in this estimate because  $U_f$  is not small compared to  $U_e$  in contradiction to our measurements. One possible resolution of this paradox is that the estimate for  $\Gamma$  is too high. However, that possibility is unlikely because even the most brittle materials (e.g., glass) have  $\Gamma \approx 3$  J/m<sup>2</sup>. Below we show that the problem lies in the assumption that the entire length of the pod must be fractured by the elastic fields.

In order to reconcile the difference between the measured and estimated fracture energy, we examined the mechanics of a single valve using a finite element model (11) with the actual geometry of a valve and a nonlinear stress-strain law selected to match the measured elastic response of a valve. The result of these calculations show that only 30% of seam's length is needed to keep the pod closed, and thus the pod is highly resistant to cracks. The latter can be quantified via Griffith's criteria: a crack will lengthen if the elastic energy per unit area gained by an advancing crack  $\mathcal{E}$  is sufficient to pay the energetic cost of creating two new crack faces (12). Fig. 2 shows a plot of  $\mathcal{E}$  calculated from the finite element model.  $\mathcal{E}$  is essentially zero for the first 70% of the seam, and therefore up to 70% of the seam can be cracked without precipitating a release of the stored energy.

While the finite element calculation shows that the seed pod is highly resistant to cracking, it does not show why this is the case. A simpler model, based on the elastica approximation (13), reveals a crucial dependence on the shape of the valve. We considered valves with triangular cross-sections and varying tapers from none (i.e., uniform thickness and width) to the actual taper of *I. glandulifera*'s valves (i.e., linearly increasing thickness and width;

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move the outer edge of the model down to the  $z = 0$  plane along a segment  $[0, s]$ . From the finite element model we calculate the energy needed to bring edges together of length  $s$ . This calculation is physically equivalent to measuring the stored energy when adjacent valves are bonded along the bottom  $s$  of their length.

**Elastica.** The energy of a valve is given by:

$$U = \int_0^L ds EI(s) (\kappa(s) - \kappa_0)^2, \quad [1]$$

where  $E$  is the elastic modulus,  $\kappa$  is the curvature,  $\kappa_0$  is the natural curvature,  $I(x) = \frac{1}{12} b(s) h(s)^3$  is the moment of inertia where  $b$  is the width of the valve and  $h$  is the thickness of the valve, and  $s$  is the arc length measured from the top. The shape of the valve is codified in  $b$  and  $h$ . Both  $h$  and  $b$  increase approximately linearly along the length of the valve (see Fig. 1), and therefore  $I = I_0(1 + s/L)^\alpha$ . The case  $\alpha = 0$  corresponds to a beam with constant height and width,  $\alpha = 1$  to a constant height and linear increase of width,  $\alpha = 3$  to constant width and linear increase of height, and  $\alpha = 4$  to a linear increase in both the height and the width (i.e., the actual geometry of the valve). We

define  $y(s)$  to be the deflection of the beam. With the approximation  $\kappa \approx d^2y/ds^2$ ,  $U$  was minimized to obtain the equation:

$$\frac{d^2y}{ds^2} = \frac{k_1s + k_2}{I(s; \alpha)},$$

where  $k_1$  and  $k_2$  are integration constants to be determined by the boundary conditions. Boundary conditions were simply supported at  $s = 0$  (i.e.,  $y(0) = 0$  and  $\frac{d^2y}{ds^2}(0) = \kappa_0$ ) and forced to lie flat at  $s = L$  (i.e.,  $y(L) = 0$  and  $\frac{dy}{ds}(L) = 0$ ). The elastica model allows the material to pass thru  $y = 0$ . Nonetheless, the requirement that the  $y = 0$  plane be impenetrable can be obtained by requiring that  $y(L - \epsilon) = 0$ . The solution is unchanged except that  $L$  is renormalized to  $L - \epsilon$ . Iterating this procedure will generate the solution  $y(x) = 0$  for all  $x$ .

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