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The seed dispersal catapult of *Cardamine parviflora* is efficient but unreliable

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**THE SEED DISPERSAL CATAPULT OF *CARDAMINE PARVIFLORA*
(BRASSICACEAE) IS EFFICIENT BUT UNRELIABLE¹**

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- *Premise of the study:* Seed dispersal performance is an essential component of plant fitness. Despite their significance in shaping performance, the mechanical processes that drive dispersal are poorly understood. We have quantified seed dispersal mechanics in *Cardamine parviflora* (Brassicaceae), a ballistic disperser that launches seeds with specialized catapult-like structures. To determine which aspects of catapult function dictate interspecific dispersal differences, we compared this disperser with other ballistic dispersers. Comparison with brassicas that lack ballistic dispersal may also provide insight into the evolution of this mechanism.
- *Methods:* Catapult performance was quantified using high-speed video analysis of dehiscence, ballistic modeling of seed trajectories, and measuring the mechanical energy storage capacity of the spring-like siliqua valve tissue that launched the seeds.
- *Key results:* The siliquae valves coiled rapidly outward, launching the seeds in 4.7 ± 1.3 ms (mean \pm SD, $N = 11$). Coiling was likely driven by the bilayered valve structure. The catapult was $21.3 \pm 10.3\%$ efficient (mean \pm SD, $N = 11$) at transferring stored elastic energy to the seeds as kinetic energy. The majority of seeds (71.4%) were not launched effectively.
- *Conclusions:* The efficiency of the *C. parviflora* catapult was high in comparison to that of a ballistic diplochore, a dispersal mode associated with poor ballistic performance, although the unreliability of the launch mechanism limited dispersal distance. Effective launching requires temporary seed-valve adhesion. The adhesion mechanism may be the source of the unreliability. Valve curvature is likely driven by the bilayered valve structure, a feature absent in nonballistic brassicas.

Key words: ballistic; biomechanics; Brassicaceae; *Cardamine*; seed dispersal; siliqua.

Seed dispersal performance is an essential component of plant fitness (Howe and Smallwood, 1982; Eriksson and Jakobsson, 1999; Nathan and Muller-Landau, 2000; Willson and Traveset, 2000; Levin et al., 2003). Through effective seed dispersal, plants can establish new populations, avoid predators and pathogens, reduce kin competition, and minimize inbreeding depression (Augsburger, 1983; Primack and Miao, 1992; Willson and Traveset, 2000; Wright, 2002). Despite its significance within plant life cycles, the physical mechanisms that underlie seed dispersal performance are poorly characterized. A better understanding of the mechanics of dispersal will clarify which factors dictate seed dispersal patterns. With this in mind, we have examined the mechanics of seed dispersal in a brassica, *Cardamine parviflora*, a ballistic disperser that launches seeds away from the parent plant. Through comparison of *C. parviflora* with other ballistic dispersers, we aim to determine which mechanical factors underlie ecologically important dispersal differences between species. Further comparison with closely related nonballistic brassicas will give insight into the morphological features required for ballistic dispersal in this group, an important step in understanding the developmental and evolutionary processes that underlie the emergence of this dispersal mechanism.

Of the many potential mechanisms, including air and water flows and carriage by animals (Willson and Traveset, 2000; Levin et al., 2003), ballistic dispersal is the most mechanically

complex (Howe and Smallwood, 1982; Stamp and Lucas, 1983; Witzum and Schulgasser, 1995; Garrison et al., 2000; Beaumont et al., 2009; Vogel, 2009), relying on mechanical energy stored in specialized fruit tissues to launch seeds (Niklas, 1992; Witzum and Schulgasser, 1995; Hayashi et al., 2009). Ballistic dispersal may be the sole mechanism, or in ballistic diplochores, serve as a precursor to secondary dispersal by other means (Beattie and Lyons, 1975; Stamp and Lucas, 1983; Ohkawara and Higashi, 1994; Webb, 1998; Garrison et al., 2000; Vander Wall and Longland, 2004; Hayashi et al., 2009). Plants entirely reliant on ballistic dispersal have been termed distance maximizers because they typically exhibit more effective ballistic dispersal than do ballistic diplochores (Stamp and Lucas, 1983). It is, however, unclear which aspects of seed catapult performance underlie interspecific differences in primary ballistic seed shadows.

Catapult energy storage and transfer has so far been measured in only one species, a ballistic diplochore, *Impatiens capensis* (Hayashi et al., 2009), in which long-distance secondary dispersal occurs via water (Trewick and Wade, 1986; Perrins et al., 1993; Tabak and von Wettberg, 2008). The catapult efficiency in this species is low. Only 0.5% of the elastic energy stored in the pod tissue is transferred to the seeds as kinetic energy during dehiscence (Hayashi et al., 2009). We hypothesized that in comparison, the catapult mechanism of a distance maximizer would have higher energy transfer efficiency and have catapult tissue that has a higher capacity for elastic energy storage.

For comparison, we quantified ballistic performance in sand bittercress (*Cardamine parviflora*). This species has the characteristics of a distance maximizer: an apparent absence of secondary dispersal, and small, smooth, dense seeds lacking the modifications present in ballistic diplochores. Similar methods

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to those used by Hayashi et al. (2009) were employed to quantify ballistic dispersal performance. Seed launch trajectories were determined by high-speed video analysis; ballistic modeling was used to predict optimal launch angles for maximizing launch distance; and the catapult mechanical energy storage capacity was determined from the force–extension relationships of catapult tissue.

The mechanisms underlying dehiscence in brassicas, particularly *Arabidopsis thaliana*, have received considerable attention (e.g., Ferrándiz et al., 2000; Liljegren et al., 2000; Ferrándiz, 2002). While dehiscent, *Arabidopsis* siliquae, like those of most brassicas, do not explosively project seeds away from the parent plant; they simply split along separation zones (Spence et al., 1996; Mummenhoff et al., 2009). *Cardamine* siliquae share many structural features with splitting siliquae (Fig. 1). The important difference is that dehiscence is accompanied by coiling of the valve tissue and seed projection (Fig. 2). Functional and morphological comparisons between *Cardamine* spp. and *Arabidopsis* spp. may therefore give valuable insight into the developmental processes that underlie the evolution of ballistic seed dispersal.

MATERIALS AND METHODS

Plant materials—Seven sand bittercress (*Cardamine parviflora*) plants with mature siliquae were collected in May 2009, at Wellesley College, Massachusetts, United States. These were immediately replanted in moist potting compost to minimize dehydration and transferred to the laboratory for video and mechanical analyses. All experiments were carried out on the day of collection.

High-speed videorecording—The pedicel of a single, mature siliqua was clamped in a hemostat, cut proximally to the clamp, and its height above the soil recorded. The siliqua was placed in the field of view of a high-speed digital videocamera (X-PRI, AOS Technologies, Baden Daettwil, Switzerland) with a Micro-Nikkor 105 mm 1:2.8 lens (Nikon, Melville, New York, USA), with its longitudinal axis perpendicular to the ground, matching the in situ orientation. A mirror above the siliqua at 45° to the horizontal provided a top view. The frame resolution and rate of the camera were set at 400 × 300 pixels and 2000 Hz, respectively. An enclosure, open on the side facing the camera, was placed over the siliqua and mirror to aid recovery of the seeds and valves after dehiscence. Dehiscence was triggered by lightly prodding the siliqua with forceps. Dehiscence videos were saved to a personal computer (Windows operating system) as AVI files through Imaging Studio (version 2.5.2x, AOS Technologies, Baden Daettwil, Switzerland). After each dehiscence, all seeds and valve coils were immediately collected and weighed.

Video analyses—Initial seed trajectories were determined from the video images using Image J (version 1.04g; Abramoff et al., 2004). Images were calibrated by placing a three-dimensional object of known size in the camera field of view. From both the horizontal and top view, the estimated center of mass of the launched seeds was tracked sequentially with respect to time in the first 2 ms after losing contact with the valve.

Not all seeds were launched effectively from the coiling valves, and they thus fell from the siliqua. These were assumed to have received no energy from the coiling valves and assigned a launch distance of 0 m. Data were collected from 11 siliquae. These contained 290 seeds in total, of which 83 were launched, the remainder falling from the siliquae.

Predicting seed dispersal distance and optimum launch angle—The seed dispersal distance and optimum launch angle of launched seeds were predicted using a ballistics computer model (Vogel, 1988). The model used an iterative approach, starting with the initial launch height and trajectory of the seed and factoring in drag, to predict the launch distance. It was also possible, for a given launch height and trajectory, to systematically change launch angle to determine the optimum launch angle for maximizing launch distance. The drag force acting on the seed (F_D) was calculated as

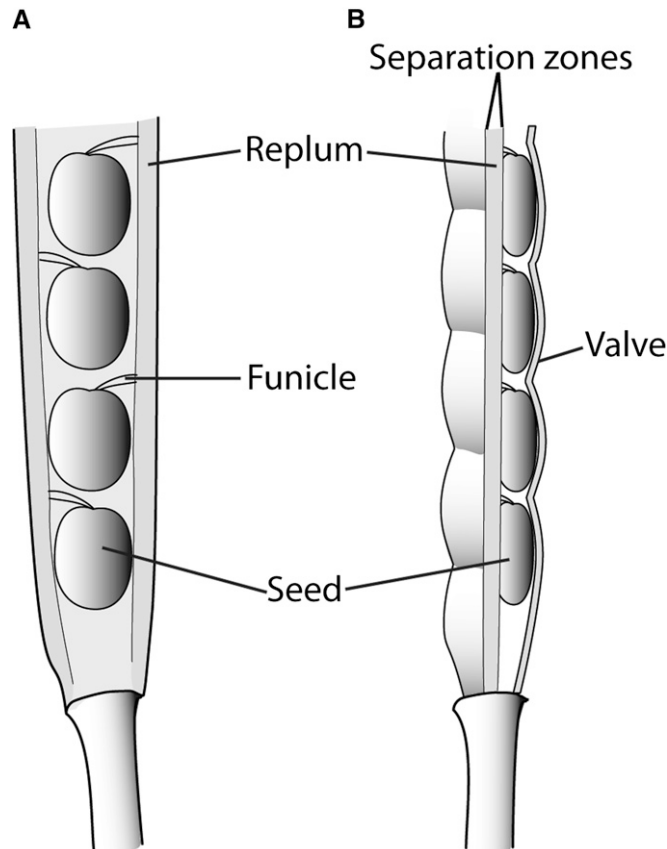


Fig. 1. Diagram showing the arrangement of seeds within the *Cardamine parviflora* siliqua. (A) Seeds in situ on repla with valve removed. (B) Lateral view with one valve shown in vertical section.

$$F_D = \frac{1}{2} \rho v^2 A C_d,$$

where ρ was air density ($\text{kg}\cdot\text{m}^{-3}$), v was velocity ($\text{m}\cdot\text{s}^{-1}$), A was the projected frontal area (m^2), and C_d was the drag coefficient. C_d is a dimensionless quantity dictated by projectile shape. For a sphere with a diameter of a millimeter and a speed of $6\text{ m}\cdot\text{s}^{-1}$, the Reynolds number is about 400, for which, a figure of 0.47 for drag coefficient is appropriate. The seed shape approximated an oblate spheroid whose frontal area varied depending on orientation. The seeds tumbled in flight, so a mean projected area was calculated from the areas projected in the x , y , and z planes. For a given seed orientation, frontal area was calculated as $A = \pi L_{\text{major}} L_{\text{minor}}$, where L_{major} and L_{minor} were the lengths of the major and minor axes of the seed in that orientation (m). Dimensions of a subsample of 20 launched seeds were measured using an electronic digital caliper (Marathon, Belleville, Ontario, Canada). Using the mean launch speed, seed mass, and frontal area, launch distances were predicted for $-90^\circ > \theta < 90^\circ$, -90° being vertically downward and 90° vertically upward relative to the horizontal. A 2nd-order polynomial was fitted to the data using the program Igor Pro (version 5.0.4.8, Wavemetrics, Portland, Oregon, USA), from which the optimum angle for maximizing distance was determined.

Stored mechanical energy, seed kinetic energy, and launch efficiency—Valve coils collected from the dehiscent siliquae were used for mechanical analyses immediately after weighing. The head of a size 1 insect pin was attached to both ends of each valve with cyanoacrylate glue (Krazy Glue, Elmer's Products, Columbus, Ohio, USA). The pins were shaped into hooks and connected to a force transducer (300B-LR; Aurora Scientific, London, Ontario, Canada). The force transducer could control valve length while measuring the force exerted by the valve tissue. Valve force was recorded while re-extending coiled valves to their predehiscence, in-situ length with a micromanipulator.

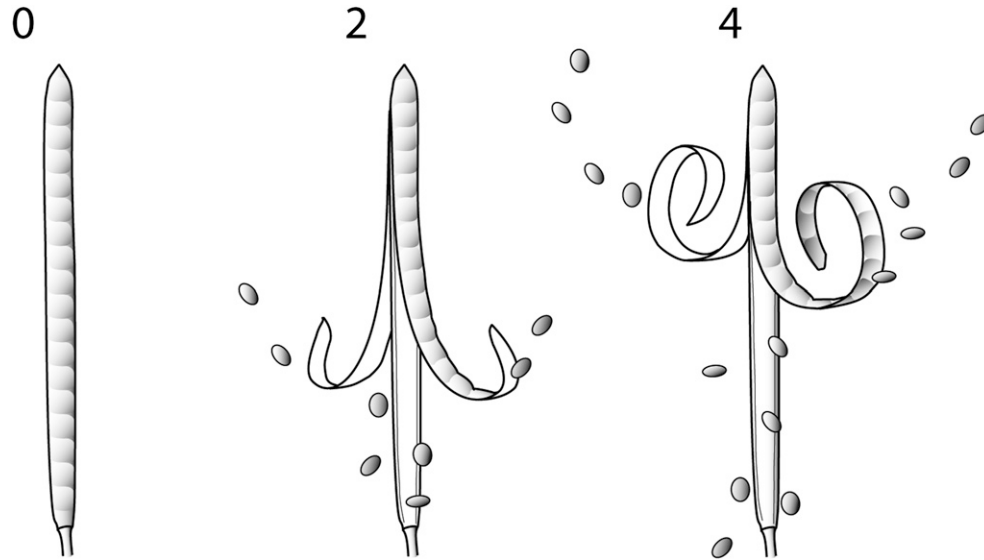


Fig. 2. Diagram showing sequential coiling of the siliqua valves and seed launch during dehiscence. Numbers show the elapsed time in milliseconds from the start of dehiscence.

The total amount of mechanical energy required, indicating the mechanical energy storage capacity (E_{valve}) of the valve was determined from the integral of the force–length relationship. When data were obtained from only one valve, the total energy stored per siliqua (E_{siliqua}) was calculated assuming that the energy storage capacity of both valves was equal.

The translational kinetic energy of the launched seed was calculated as

$$EK_{\text{seed}} = \frac{1}{2}mv_{\text{res}}^2.$$

Previous analyses determined that seed rotational kinetic energy is negligible (<0.1% of the total; Hayashi et al., 2009), so translational kinetic energy was taken to represent the total kinetic energy of the seed. The sum total of seed kinetic energy (EK_{total}) was calculated for each siliqua. The efficiency of catapult energy transfer was calculated as

$$\text{Efficiency (\%)} = \frac{EK_{\text{total}}}{E_{\text{siliqua}}} \times 100.$$

Statistical analyses—A one-way ANOVA and a Tukey honestly significant difference (HSD) post hoc test were used to test for significant differences in the mean launch distances for each siliqua. One-sample *t* tests compared measured launch angles to the optimum predicted by the ballistic model, as well as 0°, the expected mean value for a random angle distribution in the $-90^\circ > \theta < 90^\circ$ range.

RESULTS

Siliqua morphology and dehiscence—Two lateral valves, attached at their margins to the repla, enclosed the seeds (Fig. 1). Surface sutures at the valve margins marked the separation zones. The valves formed a series of pockets closely opposed to the surface of the seeds (Fig. 1B). During dehiscence, the valves coiled outward from the siliqua base, separating from the repla along their lateral margins (Fig. 2). Valve coiling took 4.7 ± 1.3 ms (mean \pm SD, $N = 11$) to complete.

Seed distribution—The majority of seeds fell from the siliquae during dehiscence, with only 28.6% being launched by the coiling valves. This launch percentage was highly variable be-

tween individuals, ranging from 6 to 63%. The distribution of predicted seed dispersal distances was heavily skewed by the high proportion of launch failures (skewness, 1.69) with a mean dispersal distance of 0.26 ± 0.51 m (Fig. 3A, mean \pm SD, $N = 290$). The mean dispersal distance of the launched seeds was 0.94 ± 0.46 m (Fig. 3B, mean \pm SD, $N = 83$). Launch distances varied significantly between siliquae (Fig. 3B, GLM, $F_{10, 73} = 7.01$, $P < 0.05$).

Launch trajectories—For seeds that were actively launched by the valves, the distribution of launch angles was skewed to the positive end of the possible range (-90° , straight down, to $+90^\circ$, straight up) (Fig. 4A). The mean of $52.2 \pm 23.9^\circ$ (\pm SD, $N = 83$), was significantly different from 0° ($t = 19.9$, $df = 82$, $P < 0.0001$), the expected mean if launch angles were random.

The mean seed launch velocity was 6.29 ± 2.73 m·s⁻¹ (\pm SD, $N = 83$, range 1.29–11.96). Using the ballistic model with this velocity and the mean launch height of 0.189 m and the mean seed mass and frontal area reported in Table 1, we determined the optimum launch angle to be 34.3° (Fig. 4B). This was significantly lower than the observed mean launch angle of 52.2° ($t = 6.8$, $df = 82$, $P < 0.001$).

Energy storage capacity of valve coils—Figure 5 shows a representative force–length curve for a siliqua valve during re-extension. The energy storage properties of the valve tissues are summarized in Table 2.

DISCUSSION

By examining the basic mechanics of ballistic seed dispersal, we can gain insight into the factors that dictate dispersal differences between species and the morphological features required for an effective catapult mechanism. Distance maximizers, reliant entirely on ballistic dispersal, are predicted to show long ballistic dispersal distances, consistent launch performance, and few launch failures (Stamp and Lucas, 1983; Ohkawara and Higashi, 1994; Narbona et al., 2005; Hayashi et al., 2009). In contrast,

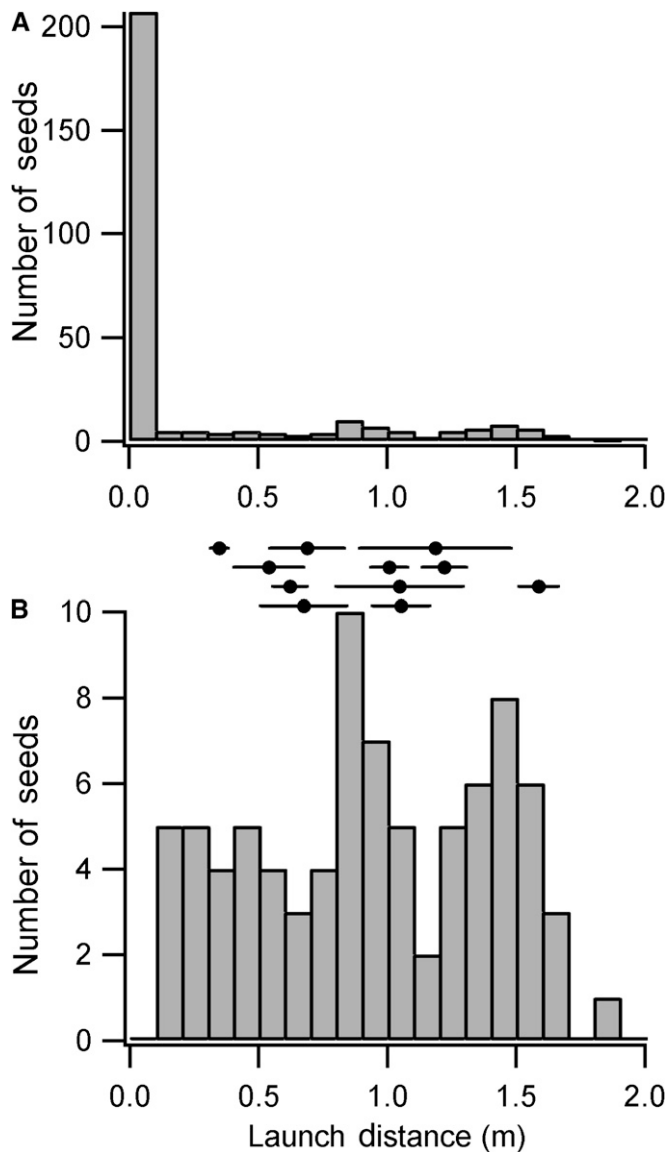


Fig. 3. Distribution of calculated seed dispersal distances. (A) All seeds including those that fell unlaunched from the siliquae ($N = 290$). (B) Seeds launched by the coiling valves excluding those that fell from the siliquae. Circles and horizontal bars show the mean and standard errors of the launch distance for individual pods ($N = 11$ pods, 83 seeds). Markers are offset so individual mean values can be distinguished.

ballistic diplochores, reliant on a postlaunch, secondary dispersal mechanism for long-distance dispersal, typically have short ballistic dispersal distances with high variability (Stamp and Lucas, 1983; Ohkawara and Higashi, 1994; Hayashi et al., 2009). We had hypothesized that differences in performance would be generated by variation in the capacity of the catapult tissues to store mechanical energy, and the efficiency with which this energy was transferred to the seeds. Contrary to our initial expectations, overall dispersal patterns in *C. parviflora*, a species primarily reliant on ballistic dispersal, and *I. capensis*, a ballistic diplochore, were similar.

Both species had highly skewed dispersal patterns, with the majority of seeds landing adjacent to the parent plant (Fig. 3A) (Hayashi et al., 2009). In both cases, the skewed dispersal is due

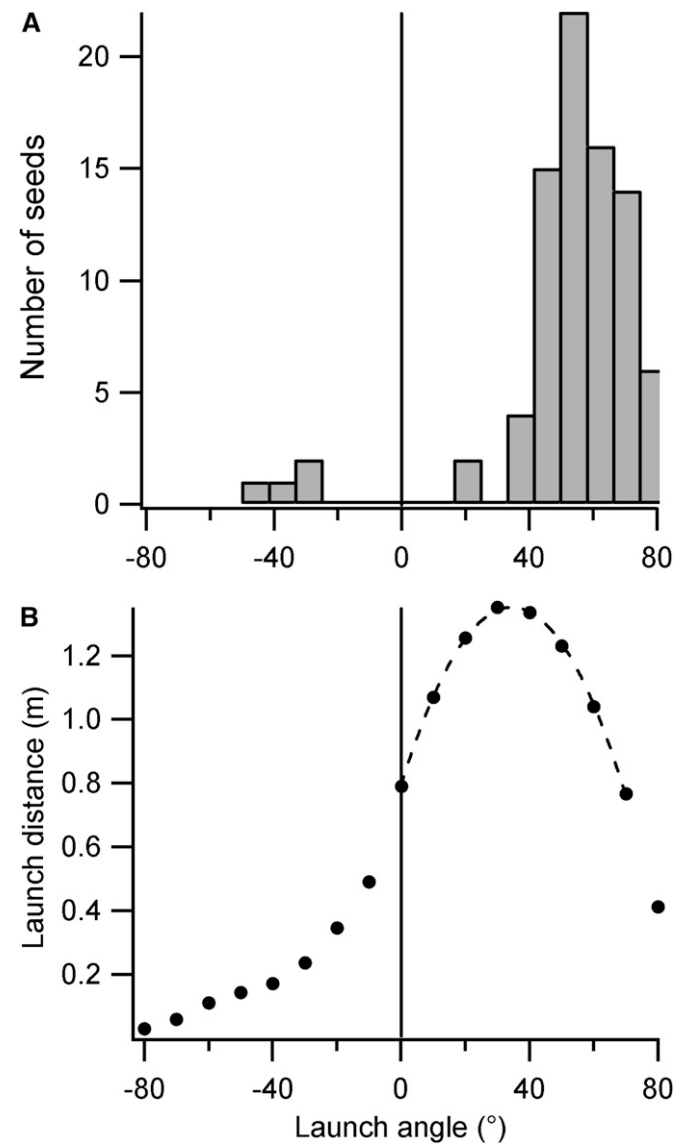


Fig. 4. (A) Distribution of seed launch angles, excluding seeds that fell unlaunched from the siliquae ($N = 83$). (B) Relationship between launch distance and launch angle for a seed with a mean mass, frontal area, and launch trajectory. Data between 0 and 70° were fitted with a second order polynomial: launch distance = $0.79 + 0.032\theta - 0.00047\theta^2$, where θ is the launch angle.

to the inherent unreliability of the catapult mechanism, with many seeds receiving little or no mechanical energy from the elastic-energy-storage structures in the fruit during launch. Despite this unreliability, the mean relative dispersal distance,

TABLE 1. Physical characteristics of *Cardamine parviflora* seeds and siliqua valves.

	Mean \pm SD (N)	Range
Mean seed mass (mg)	0.15 ± 0.09 (83)	0.10–0.19
Mean projected frontal area (mm ²)	0.31 ± 0.03 (20)	0.27–0.41
Mean number of seeds/siliqua	26.4 ± 7.6 (11)	13–35
Mean total valve mass (mg)	5.4 ± 0.3 (11)	4.8–6.4

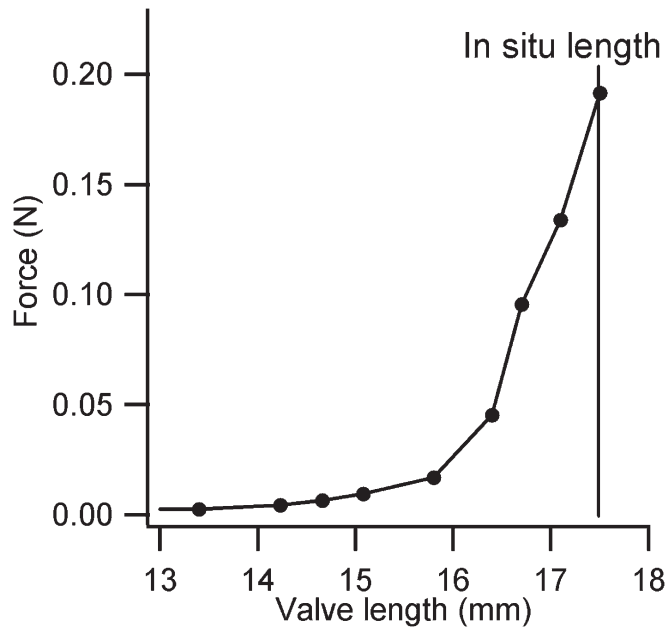


Fig. 5. Representative force-length relationship for a siliqua valve during re-extension to its original in situ length by an ergometer.

the ratio of mean launch distance to launch height, was considerably greater in *C. parviflora* (0.26 m/0.19 m = 1.37) compared to *I. capensis* (0.44 m/1.80 m = 0.24). In support of our initial hypothesis, this difference in launch performance does appear to be related to differences in catapult mechanics. Catapult efficiency, the percentage of available, stored mechanical energy transferred to the seeds during launch, was much higher in *C. parviflora* (21.3%; Table 1) than *I. capensis* (0.5%) (Hayashi et al., 2009). This high efficiency compensated for a lower mechanical energy storage capacity (89 J·kg⁻¹ of valve tissue fresh mass, compared to 124 J·kg⁻¹ in *I. capensis*). For both species, the estimated catapult efficiency is based on a comparison of seed kinetic energy with the available stored elastic energy measured under quasi-static conditions. An efficiency could also be determined by comparing seed kinetic energy with the total kinetic energy in the system, including that of the coiling and occasionally launched valves. This comparison was not possible in the present study because the video images lacked the resolution to accurately track the rapidly coiling valve structure.

For the launched seeds, there was also some evidence of increased “tuning” of the launch angle, relative to *I. capensis*. Although mean launch angle was nonrandom in both species, being constrained overall to an upward trajectory, the variation in launch angle was lower in *C. parviflora* (standard deviation

of 12.8 vs. 34.9 in *I. capensis*). The launch angle was, however, significantly steeper than the optimal angle for maximizing distance (52.2° vs. 34.3°). *Cardamine parviflora* has multiple stems and grows in dense stands. The proximity of dense vegetation has been shown to significantly reduce ballistic dispersal performance (Thiede and Augspurger, 1996). The steep launch angle may therefore be adaptive in that it would reduce the likelihood of seed collisions with adjacent plants.

The ballistic dispersal mechanism in *C. parviflora* is highly variable. There are significant differences in performance between siliquae (Fig. 3B), and many seeds fall from the pods rather than being launched. *Geranium maculatum* displays what is considered the more typical distribution pattern for a species entirely reliant on ballistic dispersal: a normal distribution of dispersal distances with an impressively high relative dispersal distance (3.02 m/0.06 m = 50.3; Stamp and Lucas, 1983) and few launch failures. Comparison of the launch mechanisms in these species provides some indication as to why launch performance is so variable in *C. parviflora*.

Geranium maculatum seeds are cupped by fruit tissue (Yeo, 1984), explaining the absence of launch failures in this species, because valve–seed contact is consistently maintained during dehiscence. There are no such direct mechanical connections between seed and valve in *C. parviflora* (Fig. 1). Despite this, the launched seeds are pulled away from the repla by the coiling valves and launched upward and away from the siliqua (Fig. 2). For launching to occur, there must be temporary adhesion between seed and valve that is broken as the seed is launched. The adhesive mechanism may be a form of wet adhesion, a collective term for mechanisms that resist the relative movement of surfaces separated by a fluid film. Wet adhesion takes two primary forms, both of which can operate in the same system: Stefan adhesion in which the viscosity of the fluid resists the relative movement of two surfaces, and capillary adhesion, where surface tension at the interface between the fluid and air resists separation (Vogel, 1988, 2009; Denny, 1993).

Direct evidence for these mechanisms would be difficult to obtain because adhesion cannot be observed in situ without triggering dehiscence. It is clear however that moisture is required because there is no adhesion between dry seeds and valves (M. Hayashi, unpublished observation). This observation also excludes an alternate adhesive mechanism, which requires no fluid, van der Waals adhesion, which is caused by the interactions of molecules in closely opposed surfaces.

Successful launching requires that the adhesive force be broken as the valve coils. The degree of adhesion between surfaces is proportional to the contact area in the case of Stefan adhesion or to the perimeter of the air–water boundary in the case of capillary adhesion (Grenon and Walker, 1981; Denny, 1993). Because the valves coil during launch (Figs. 1, Fig. 6), this action would tend to produce a peeling effect. Increasingly tight coiling of the valve would progressively reduce contact between seeds and the valves, and therefore both contact area and the perimeter of this area (Fig. 6). The requirement for tight coiling to break adhesion would also favor an outward and upward seed launch trajectory because seed release would be delayed until late in dehiscence when the valves were most tightly coiled (Fig. 6). The adhesive force would be highly sensitive to variation in the amount of moisture on the inner surface of the valve and may explain the inherent performance variability—small differences in the moisture content of siliquae or within a single siliqua could lead to launch failure. Further variability may also be introduced by differences in seed position along

TABLE 2. Storage and transfer of mechanical energy by *Cardamine parviflora* siliqua valves.

	Mean ± SD (N)	Range
Mean estimated stored elastic energy/siliqua (μJ)	482 ± 219 (11)	226–824
Mean mass specific energy density (J·kg ⁻¹)	89.3 ± 40.5 (11)	41.8–154
Mean total kinetic energy transfer/siliqua (μJ)	84.2 ± 8.4 (11)	5.90–277
% of stored energy transferred to seeds	21.3 ± 10.3 (11)	1.3–43.6

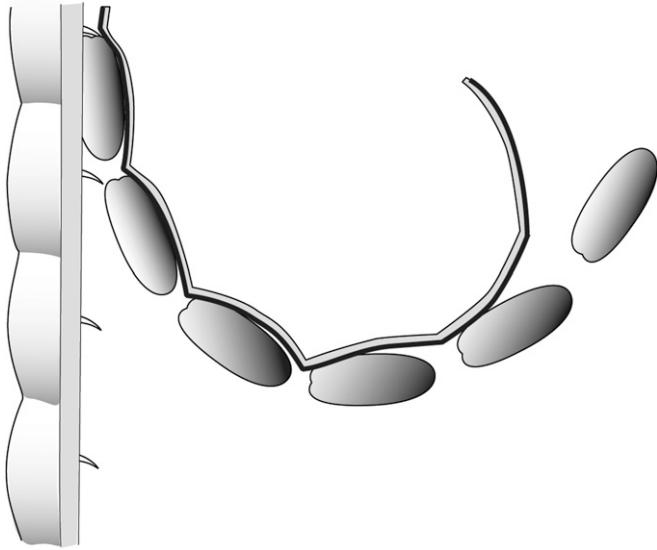


Fig. 6. Diagram of the proposed seed launch mechanism. A silique is shown in lateral view with one valve sectioned vertically. The heavy black line indicates the location of moisture on the inner surface of the valve.

the silique. Distal seeds close to the point of valve detachment must receive little energy from the coiling valve because they can only be moved a short distance during coiling (Fig. 2).

Comparisons between dehiscent and indehiscent brassica siliques have provided valuable insights into the developmental and physiological processes and structural features that underlie this mechanism (e.g., Liljegren et al., 2000). Similarly, comparisons of ballistic dispersers with related species that lack this mechanism may clarify the developmental and evolutionary processes that shape the emergence of effective plant catapults. Most dehiscent brassica siliques rely on valve tension created by shrinkage during drying to pull the valve margins away from the repla, triggering dehiscence (Spence et al., 1996). Dehiscent brassica siliques share several anatomical features: a lignified *en b* valve endocarp layer; lignified valve margins, and a nonlignified separation layer between the valve margin and lignified vascular bundles in the repla (Spence et al., 1996; Mummenhoff et al., 2009). Drying is thought to create tension in the *en b* layer and valve margins (Spence et al., 1996). This tension, combined with weakening of the middle lamella in the separation layer by enzymatic activity is the basis for dehiscence (Ferrándiz et al., 2000; Liljegren et al., 2000; Ferrándiz, 2002). In many brassicas, dehiscence is not accompanied by valve coiling, seed adhesion to the valve, or the projection of seeds away from the silique. The silique simply splits along the valve margins, the valves remain straight, and the seeds fall from the silique, with dispersal possibly being aided by wind (Spence et al., 1996).

Coiling *Cardamine* valves share the basic structural features of brassica species that have splitting dehiscence. The primary difference is the presence of a persistent *en a* endocarp layer forming the inner valve surface in contact with the seeds (Vaughn and Bowling, 2009). This layer degenerates during pod maturation in siliques that split (Spence et al., 1996). The *Cardamine en a* layer is rich in mucilaginous polysaccharides (Vaughn and Bowling, 2009), similar to those found in the G-fibers of tension wood. Tissues of this type swell by adsorb-

ing water (Bowling and Vaughn, 2008, 2009). The interaction of the *en a* and *en b* layers may be the basis for valve coiling.

Curvature in plant tissues can be created by tissue bilayers in which the adjacent layers have contrasting mechanical properties (Witztum and Schulgasser, 1995). For example, in many herbaceous plant stems, external tissues form a tensile envelope that holds internal tissue in compression (Niklas, 1992; Niklas and Paolillo, 1998). Excision of stem quadrants releases this tension, creating curvature as the outer tensile layer shortens and the formerly compressed internal tissues expand. A similar mechanism may operate to create valve curvature in *Cardamine* spp. Retention of moisture by the inner mucilage layer would result in differential drying of the valve tissues. The tensile, lignified *en b* layer could hold the swollen *en a* mucilage layer in compression. If so, release of tension during dehiscence would allow shortening of the *en b* tissue coincident with expansion of the *en a* layer, driving the outward coiling seen in the high-speed video images (Fig. 2). The inner mucilage layer would also favor retention of moisture at the valve inner surface and wet adhesion between seeds and valve.

Indirect evidence for this coiling mechanism comes from two observations. First, mature siliques, oven-dried before attempting to trigger dehiscence, split rather than coil during dehiscence, suggesting that in the absence of moisture, differential forces and coiling are abolished. Second, the straight, dried valves of these siliques curve outward if placed in water for several minutes, suggesting that the inner valve layer swells, primarily in parallel with the long axis of the valve. Confirmation of this mechanism requires detailed investigation of the cell wall anatomy of the *en a* and *en b* layers. Cells in tension-resisting plant tissues typically are elongated in parallel to the direction of the tensile stress and the cellulose microfibrils within their cell walls are oriented parallel to the long axes of the cells. This type of anatomy would be predicted for the *en b* layer. The *en a* layer may have microfibril orientations that largely constrain mucilage-driven expansion to the silique longitudinal axis.

Conclusions—*Cardamine parviflora*, despite being primarily reliant on ballistic seed dispersal, did not show the seed dispersal performance predicted for a ballistic distance maximizer. The overall ballistic dispersal pattern was more similar to the skewed distribution of a ballistic diplochore. Despite this similarity, relative dispersal distance and catapult efficiency (21.3%) were much higher than previously measured in the diplochore *I. capensis*. The catapult mechanism involves rapid outward coiling of the silique valves, likely driven by the bilayered valve structure. This bilayer arrangement is the primary structural difference between *C. parviflora* silique valves and those of dehiscent but nonballistic brassicas. Seed launch requires temporary adhesion to the valves during coiling, which may be achieved via a wet adhesion mechanism that is broken by peeling as the valves coil, releasing the seeds. Sensitivity of the adhesion mechanism to variation in valve moisture content may explain the high variability in launch performance between siliques.

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