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Putting a New Spin on the Flight of Jabillo Seeds

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Abstract:

Our paper describes the explosive seed dispersal of the *Hura crepitans* fruit. Through high-speed video analysis of an exploding fruit, we observe that the seeds fly with backspin as opposed to topspin, which was previously assumed. Backspin orients seeds to minimize drag during flight and consequently increases dispersal distance. The seeds' dispersal distance is estimated by using results from the seeds of *Ruellia ciliatiflora,* which are similarly shaped but approximately 10 times smaller than those of *Hura crepitans*. We note that the effects of lowering drag on the dispersal distance are more pronounced at higher speeds. We also see that the effect of launch height on the dispersal distance of the seeds becomes less consequential at higher launch speeds. We conclude that the increased dispersal distance due to flying with backspin should improve fitness in colonizing new habitats or escaping disease or predation and that comparisons of the seed dispersal mechanisms across species within the Euphorbiaceae and Acanthaceae might help reveal the adaptive significance of this behavior.

Introduction:

Seed dispersal underlies the fate of a plant's fitness. Plants are sessile, and seed dispersal offers a rare opportunity for movement. Successful dispersal facilitates the colonization of new niches, escape from competition against kin and accompanying pathogens, and directed movement to desirable microhabitats (Howe & Smallwood, 1982; Santos, 2006; Wenny, 2001). The three vectors in which plants are dispersed - abiotically (wind, water, and gravity), biotically

(animals), and ballistically - have significant consequences on recruitment (Levin et al., 2003; van der Pijl, 1982; Wandrag et al., 2017). Previous studies have identified that seed shadows and Population Recruitment Curves in tropical environments tend to an outward shift; this suggests distance-dependent survival in tropical plants (Connell, 1971; Janzen, 1970).

Hura crepitans is commonly known as jabillo, sandbox tree, monkey's dinner bell, and dynamite tree, the latter two names referring to the sound its fruit makes during dehiscence. It is a neo-tropical hardwood belonging to the Euphorbiaceae family (Madrigal, 2011). Native to North and South America, it is highly successful as it has been naturalized in northern Australia and is invasive to eastern Africa (The East African Network for Taxonomy, n.d.). *H. crepitans* is easily distinguished by its large size, reaching upwards of 40 to 50 m tall with a girth of more than 1 m, and for the short conical spears studding its trunk. The sap or latex of the sandbox tree can cause contact dermatitis and temporary blindness in humans who work with the wood, such as canoe builders (Madrigal, 2011).

The fruits are pumpkin-shaped capsules with an observed 12 to 16 carpels radially arranged around the stem and are approximately 6 cm in diameter (Fig. 1b). Immature fruits have a thick green dermal layer, and as fruits mature, the dermal layer dries into a thin brown covering, and the seeds detach so that one can hear rattling upon shaking the fruit. As the fruit dries, stress builds up in the carpels, eventually causing dehiscence of the capsule, and launches seeds at speeds up to 70 m/s (Swaine & Beer, 1977) to distances of up to 45 m (van der Pijl, 1982).

The explosive seed dispersal mechanism was examined carefully by Swaine and Beer (Swaine & Beer, 1977) in the first study to record images of the explosive seed launch and relate its dynamics to the seed dispersal range. In this study, the authors used a stroboscopic technique

to image seeds in flight 300 times per second. From these images, they found that seeds are ejected radially outward, with each disk rotating in the plane defined by the fruit's axis of symmetry and the seed's trajectory. The authors measured the seeds to have topspin (clockwise rotation for a projectile moving to the right). However, we show, using a modern high-speed video camera, that this observation was incorrect due to a systematic aliasing error that arose from an insufficient flash rate of the stroboscope. Instead, seeds have backspin, which keeps them oriented to minimize their drag during flight and consequently increases dispersal distance (Cooper et al., 2018).

Field Site, Materials, and Methods

This work took place at the Firestone Center for Restoration Ecology in Dominical, Puntarenas, Costa Rica in March of 2019. Fruits were harvested from young trees (Fig. 1a) in the lowland section of the adjacent Hacienda Barú Wildlife Preserve by guides in late January. The mature fruits were held in a freezer onsite until we arrived to record their opening. Fruits were brought to ambient temperature overnight and studied the following day. Of the six fruits, one exploded overnight, and the others were triggered with hot air from a heat gun (Figure 2). Fruits would typically explode within about 10-20 minutes from when the heat was applied. Explosions were recorded with a Vision Research Miro 311 camera at frame rates of 2000 fps with a 100 microsecond exposure time under ambient sunlight. Seed velocities were calculated by hand using LoggerPro 3.16 (Vernier Inc, Beaverton, OR) to measure the displacement of seeds between subsequent frames. We were able to acquire only a single video, Video 1, in which the seeds were ejected and recorded by the camera.

Results:

The energy to launch seeds comes from internal strains that build up in each of the carpels (See Fig. 1c). This strain acts to open the carpels (CP) at the distal end (D) while the proximal end of a carpel (P) stays fused together and in contact with its enclosed seed. Before the explosion, the carpels are restrained by their nearest neighbors. However, upon drying, the carpels separate from one another and the fruit begins to split. Once a single carpel opens and begins to slide away from its neighbors, the rest are free to move, and there is a sudden outward motion of all the carpels at once. Since the distal (top) part of the carpel, (D), opens during this release of strain, it moves radially away from the axis of the fruit and causes the carpel to rotate in such a way that a carpel ejected from the right side of the fruit will rotate clockwise. The subsequent motion of the base of the carpel imparts momentum and rotation to the seed in contact at (P), which flies out through the now open distal end (D). For the previous example of a carpel on the right of the fruit, the seed acquires a momentum upwards and to the right with a counterclockwise rotation (backspin), as one can see in Fig. 2 and Video 1. For the 5 seeds where the rotation was clear in the video, we measure an average rotation rate of 80 ± 10 Hz.

To estimate the dispersal distance of the seeds ejected by the fruits of *Hura crepitans,* we need to know the initial velocity of the seeds and the ballistic parameter, $k = \frac{|a|}{v^2}$, where a is the acceleration due to drag and v is the speed. This parameter is related to the drag coefficient, C_D, by the relation $k = \frac{\rho A C_D}{m}$, where A is the area of the projectile of mass m and ρ is the density of air. To estimate k, we can use previous results from *Ruellia ciliatiflora* (Cross 2013), which have similarly shaped seeds that are approximately 10 times smaller than those launched by *H. crepitans* (Table 1). If we assume that these similarly shaped seeds flying at similar Reynolds numbers (10^3 vs. 10^4) share the same drag coefficient, then we can relate their ballistic

parameters through, $k_H = \frac{A_H m_R}{A_R m_H}$, where m is the mass of the seed and the subscripts H and R indicate *Hura* and *Ruellia* respectively. From this formula, we estimate k_H to be approximately 0.03 m^{-1} or about 1/7 that of *R. ciliatiflora*, which has a mean value of 0.2 ± 0.1 m^{-1} for spinning seeds (mean ± S.D., $N = 59$) (Cooper 2018). By examining the flight of the seeds moving most perpendicularly to our line of sight, we estimate from our video that the launch angle (from horizontal) is approximately 30° with a launch speed of approximately 13 m/s.

Analysis and Discussion:

Our video confirms a number of the previous observations made by Swaine and Beer but also helps refine some of their claims about seed dispersal. The first difference is that, with our enhanced frame rate, we see that seeds fly with backspin as opposed to topspin, as was previously surmised. Seeds flying with backspin minimize the drag force by minimizing their frontal area, which can increase dispersal range (Cooper et al. 2018). This behavior has been observed across many Acanthaceae species (Cross 2013), but this is the first time this behavior has been documented outside of that family. The choice of assigning topspin instead of backspin was essentially arbitrary in the previous study since the low strobe rate made it impossible to resolve the direction of rotation.

Since the rotation rate of the seeds was comparable to the flash rate of the stroboscope (300 Hz), the values they recorded can be corrected by subtracting the measured rate from the strobe rate. The uncorrected numbers from Swaine and Beer incorrectly show that faster projectiles were rotating more slowly than slow ones. When we correct their data accordingly, we find that there is a linear relationship between rotation rate and speed that is consistent with our single data point (Fig. 3).

Rotation axes other than backspin are unstable and will tend towards backspin through any small deviation in the angle of attack. This instability comes about from the combination of aerodynamic forces and gravitational forces coupled with the gyroscopic motion of a spinning disk. Any non-zero angle of attack results in the disk acting like a pitched airfoil, which experiences an associated torque and lift whose directions depend on the sign of the pitch angle. The lift will act to change the angle of attack as the disk acquires an upward velocity while keeping its rotation axis and thus plane of rotation the same. At the same time, the torque will cause the spinning disk to precess about the direction of motion. As the disk precesses, the direction of its lift will vary, and it will make a banked turn similar to the motion of a boomerang, resulting in what can be a small dispersal range despite a long flight distance. In contrast, a seed with backspin is stable and small deviations in the angle of attack, such as the wobbling seeds seen in Fig. 2, are self-correcting such that the wobble will damp out over time. The reader is encouraged to see this for themselves by throwing a CD or DVD with spin.

Swaine and Beer did not account for the streamlined orientation of a spinning seed and consequently overestimated the ballistic parameter by nearly a factor of four. Their number is, however, a good estimate for a seed without spin that would tumble during its flight, and the factor of four increase in the ballistic parameter is in line with the difference in drag seen between spinning seeds and flopping seeds in Cooper et al. 2018. In Fig. 4, we plot the range of both spinning and tumbling seeds as a function of launch speed and height for a typical 30° launch angle by numerically solving the equations of motion using MATLAB 9.8 (Mathworks, Natick, MA).

The plot shows that the effects of lowering drag on launch range are more pronounced at higher speeds. For the tumbling seeds, the gain in range with launch speed becomes marginal for speeds above about 20 m/s while for the spinning seed the launch range is still increasing with speed up through 45 m/s. As an example, a seed launched from a height of 3 m at a speed of 13 m/s will travel 9 m compared to 7 m for a seed that tumbles. However, for a seed launched at 43 m/s (the mean launch speed recorded by Swaine and Beer), we estimate ranges of 41 m and 17 m for a spinning and tumbling seed, respectively. It is likely the power of the explosion in our video was compromised by the cold storage of the fruit before we arrived to record them and that the launch speeds recorded in Swaine and Beer are more accurate for explosions in nature.

It is also evident from the graph that launch height is not a significant factor in increasing dispersal range and becomes less important as the launch speed increases. The relative advantage gained from height also decreases with launch speed. This observation is true for any projectile with drag and applies to any plant using ballistochory. This behavior has been reported across a wide variety of plants from shrubs to trees (Stamp and Lucas 1983, van der Burgt 1997) including Euphorbiaceae shrubs (Narbona et al. 2005) as a primary (Swaine et al. 1979) and in combination with a secondary (Stamp and Lucas 1983) dispersal mechanism. Given the relatively small advantage of a higher launch height for ballistically dispersed seeds, it is interesting *H. crepitans* and other ballistochoric trees adapt this dispersal vector, compared to wind-dispersed trees where such added height provides a clear advantage in ambient wind (Gregory 1973) and time aloft. More studies are needed to understand the adaptive significance of ballistic seed dispersal.

Conclusion:

We have observed that the fruits of *H. crepitans* launch their seeds with backspin, which acts to dynamically keep the seed in its most streamlined orientation during flight and is predicted to more than double the range compared to a seed that tumbles. This enhanced dispersal range should improve fitness in colonizing new habitats or escaping disease or predation compared to a seed launched without spin. This behavior has been observed previously in *Ruellia ciliatiflora,* where it evolved independently. Comparisons of the seed dispersal mechanisms across species within the Euphorbiaceae and Acanthaceae might help reveal the adaptive significance of this behavior.

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Figure 1: *Hura crepitans.* (a) A nearly bare *H. crepitans* tree from which fruit was harvested. These trees lose their leaves annually before flowering (Jack Ewing, private communication 2020) Inset: a vertically presenting fruit in the tree. (b) The distal (above) and proximal view of a mature fruit collected from the ground. Scale bar = 1 cm. (c) A seed (S) and carpel (CP). The seed escapes from the distal end (D). Its last point of contact is at the proximal end (P). The red arrows indicate the rotation of the seed and carpel post-explosion.

Figure 2: A composite image of seeds as the exploding fruit launches them from a 2,000 fps video. The blue dots allow one to track the backspin. Each image is 4.5 ms apart.

Figure 3: Scatter plot of angular velocity vs. launch speed for *Hura crepitans* seeds. We correct the aliasing error present in two of Swaine and Beer's data points and show that our single data point is consistent with the linear trend in the corrected data. The linear trend between angular velocity and launch speed is also consistent with the linear trend that was found in Cooper et al. 2018 for *Ruellia ciliatiflora* seeds.

Figure 4: Dispersal range vs. launch speed for seeds launched at 30° above horizontal at a series of launch heights from 1 to 21 m in 2 m increments. The two sets of lines correspond to calculated ranges for low drag, spinning seeds ($k = 0.03$ m^{-1}) and higher drag, tumbling seeds ($k = 0.12$ m^{-1}).

Video: A video of the explosion of *H. crepitans* fruit recorded at 2,000 fps.

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338x154mm (300 x 300 DPI)

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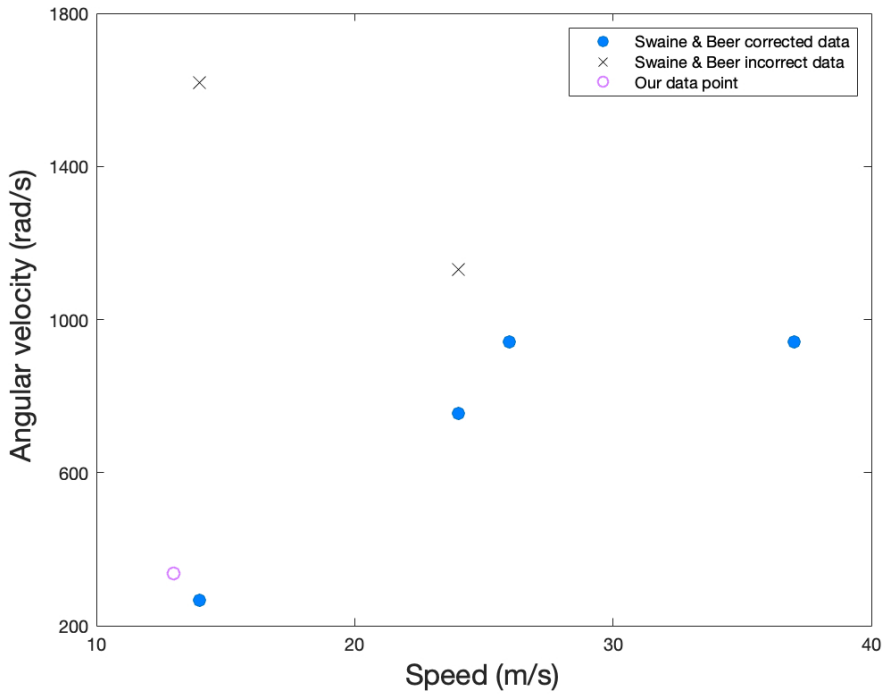

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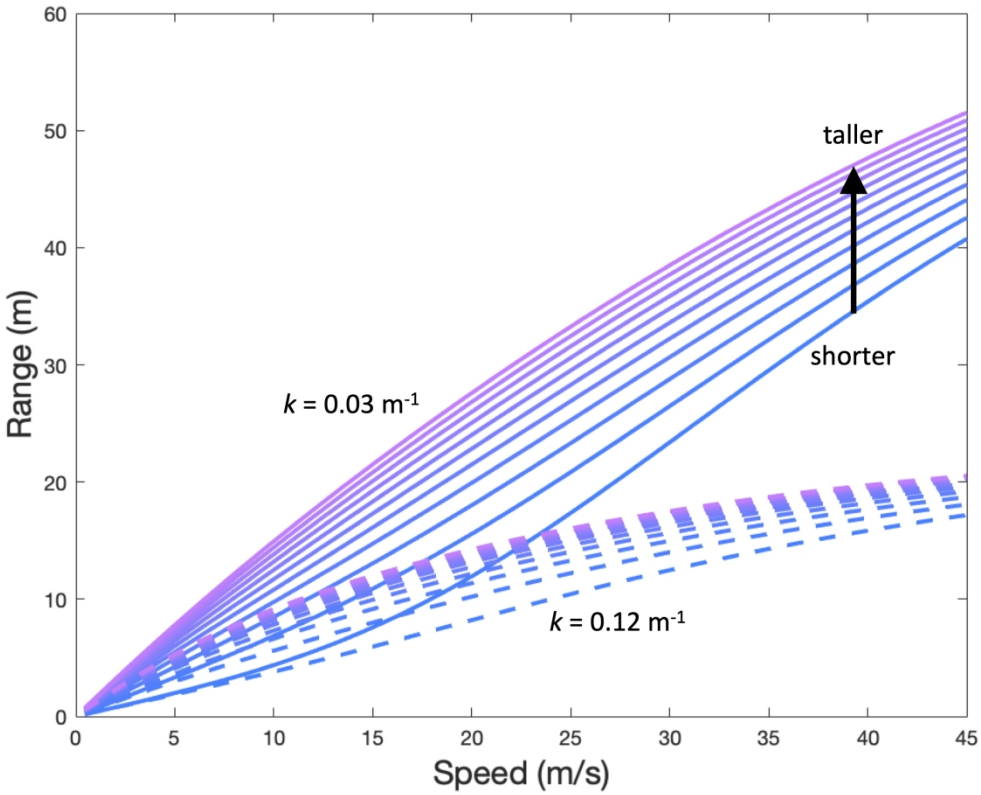
395x296mm (72 x 72 DPI)



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220x176mm (300 x 300 DPI)

Species	Mass (g)	Major axis (mm)	Minor axis (mm)	Thickness (mm)	Reynolds number
Hura crepitans (mean ± S.D., N = 17)	1.2 ± 0.1	22 ± 1	19 ± 1	5.3 ± 0.3	10^3
Ruellia ciliatiflora (mean ± S.D., N = 10)	0.0017 ± 0.0002	2.7 ± 0.2	2.35 ± 0.08	0.46 ± 0.06	10^4

Table 1: Comparing *Hura crepitans* seeds with those of *Ruellia ciliatiflora. H. crepitans* seeds are roughly 10 times larger than their *R. ciliatiflora* counterparts and, therefore, cover a 100 times larger frontal area. The mass of *H. crepitans* is also roughly 1000 times larger than that of *R. ciliatiflora*, consistent with their volume ratio.