Wind Dispersal of Eastern Redbud, *Cercis canadensis* Linnaeus (Fabaceae), Seedpods[1]

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"About 30 years ago there was much talk that Geologists ought only to observe & not theorise; & I well remember some one saying, that at this rate a man might as well go into a gravel-pit & count the pebbles & describe their colours. How odd it is that every one should not see that all observation must be for or against some view, if it is to be of any service." Darwin (1861)

Abstract: The eastern redbud, *Cercis canadensis*, is a small tree native to eastern North America that has become a commonly used ornamental in the United States and worldwide. We used laboratory experiments to test whether the seedpods of eastern redbuds are wind dispersed by exposing them to pulses of air blowing at different wind speeds. Rush milkweed, *Asclepias subulata*, seeds, which have morphological modifications that make them truly wind dispersed, were used for comparison. At all speeds tested (0, 25, 35 km/h), at a height of 190.5 cm above the ground, the seedpods of *C. canadensis* remained airborne much for a shorter time than the seeds of *A. subulata*. At all wind speeds tested, eastern redbud seedpods were minimally wind dispersed. Among all variables measured (wind speed, seedpods, mass, length, width, and area), wind speed explained approximately 0.28 (linear regression) of the seedpod dispersal.

Key Words: Dispersule, wind dispersal, wind dispersion, *Cercis canadensis*, Fabaceae, *Asclepias subulata*, Asclepiadaceae

Introduction

Knowing how organisms disperse is essential for conservation strategies (Cowen 1990, Strykstra et al. 1998, Houghton et al. 2020, particularly amidst global climate change, West 2018) and for understanding one of the major forces of evolution, the moving of organisms (or parts of them) via migration. Besides vegetative dispersal, reproductive structures, such as spores (bryophytes and pteridophytes) as well as pollen and seeds (gymnosperms and angiosperms) are also units of dispersal, or

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dispersules (e.g., Strykstra et al. 1998). Spores and pollen are transported by wind, animals, or water.

Cercis canadensis (Linnaeus, 1753) (Fabaceae), commonly known as eastern redbud or eastern North America redbud (Figure 1), is a small tree (generally fewer than 15 m tall) native to the eastern half of the United States and southeastern continental Canada (Dickson 1990), although it appears to be uncommon in the latter. In most of its native range, where the tree is relatively common in forest understories, eastern redbuds produce insect pollinated flowers early in the year (in southern Pennsylvania, in April to May, Figures 1A and 1B), thereafter, develop cordate leaves (Figure 1C) that abscise in the fall. Seedpods mature, turning from green to dark brown, and remain attached to stems during the rest of the year in which they were formed and often up to the early spring of the following year (Figure 1C).

Eastern redbuds reproduce sexually by seeds, which are born in flattened fruits, known as seedpods or legumes. Although the shape of the seedpods and seeds lack obvious wind-dispersal structures, Krugman et al. (1974) and Dickson (1990) suggested that the seeds are wind dispersed. Because the seedpods of *C. canadensis* almost invariably fall undehisced (JASB, personal observations; Dustin Stoll, personal communication to Santiago-Blay, January 17, 2023), we assumed that Krugman et al. (1974) and Dickson (1990) meant that the seedpods, carrying the seeds, are the dispersal units or dispersules. This interpretation was confirmed by Dickson (personal communication to Santiago-Blay, March 15, 2023).

Herein, we tested the wind dispersal hypothesis for redbud seedpods. The null hypothesis is that *C. canadensis* seedpods stay airborne under different wind speed conditions as much as true wind dispersed structures, such the seeds of *Asclepias subulata*. The alternative hypothesis is that *C. canadensis* seedpods do not remain airborne as much as wind dispersed seeds. Because the focus of this paper is *C. canadensis* seedpods, we measured how much the seedpods of *C. canadensis* disperse under different wind speed conditions.

Methods

Study organisms. On January 15, 2023, sixty seedpods of *C. canadensis* (Figure 2A) were selected among a much larger cohort collected on 19 December 2022 from two trees located in front of 2801 Concord Road in Springettsbury Township (York County, Pennsylvania, USA; latitude 39.982807, longitude -76.668805). The seedpods were kept refrigerated until the beginning of the experiments.

For comparison, seedpods of *A. subulata*, whose seeds (Figure 2B) are fluffy, light, and wind dispersed, were collected at the campus of the University of Arizona (Tucson, Arizona, USA; latitude 32.230507, longitude -110.951992) on February 14, 2023, and were used shortly after their arrival. Exemplars of other wind dispersed propagules (seeds or fruits), such as seeds of the common dandelion, *Taraxacum officinale* (Linnaeus) Weber *ex* F. H. Wiggers, *Matricaria* sp. (both Asteraceae) or of the American sycamore, *Platanus occidentalis* Linnaeus (Platanaceae) as well as wind dispersed fruits, such as the samaroid schizocarp of maples (*Acer* sp., Sapindaceae) or the samaras of elms (*Fraxinus* sp., Oleaceae) were not available to us at the time of the experiments. All the seeds of *A. subulata* were destroyed after the conclusion of the experiments.

Figure 1. Eastern North America redbud, *Cercis canadensis* Linnaeus, 1753 (Fabaceae). A. Tree in bloom. Photo taken at the Duke Forest Korstian Division, Durham, North Carolina, USA by Dcrjsr. Date: March 16, 2012. CC-BY-3.0. https://commons.wikimedia.org/wiki/File:Cercis_canadensis_redbud_tree_bloom.jpg . B. Close-up of *C. canadensis* flowers. Photo taken by Richard Turcotte. Morgantown, West Virginia, USA. Date: April 18, 2023 (photo courtesy Richard Turcotte, USDA Forest Service). C. Close-up of leaves and seedpods. Photo in panel C taken at Nixon Park, York County, Pennsylvania, USA by author JASB. Date: October 18, 2023. Copyright of image in panel C by JASB.

The eastern redbud seedpods length and maximum width were measured (in mm) with a digital caliper (General® Ultra Tech™ No. 1433); their mass (in grams) was measured with calibrated analytical scales [Entris (Sartorius Lab Instruments, Göttingen, Germany) and New Classic ML (Mettler Toledo, Greifensee, Switzerland].

We selected seedpods of similar size. The mass of the eastern redbud seedpods and of the rush milkweed seeds, including their floss (Evangelista 2007), were recorded before and after the conclusion of all experiments to account for any weight lost during the experiments. On average, the Eastern redbud seedpods were 64.7 mm long (sd = 5.9, se = 0.8), 11.9 mm. maximally wide (sd = 0.6, se = 0.1), and their average mass was 0.102 g (measured before the tests, sd = 0.039, se = 0.005). On average, *C. canadensis* seedpods lost only about a 1.1% of their mass after the experiments. On average, the mass of *A. subulata* seeds was 0.007 g before the tests (sd = 0.002, se = 0.001). The mass of *A. subulata* seeds was not weighed after the experiments.

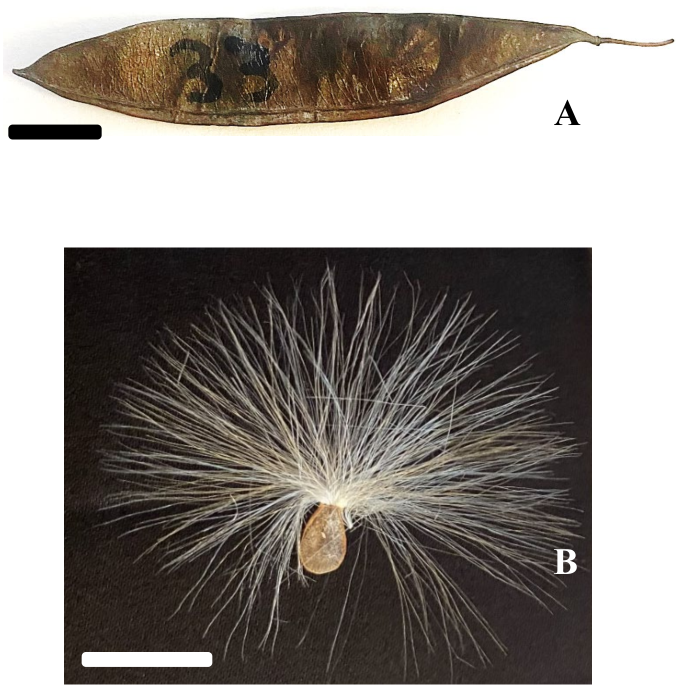

Figure 2. Dispersal units. A. *Cercis canadensis* seedpod. B. *Asclepias subulata* seed. Scale bars represent 1 cm. Photos taken by author KO.

Experimental conditions. To minimize air disturbance, these experiments took place inside a long, leveled hallway of a college building during some Saturday and Sunday afternoons, from January to March 2023 [wind speed in hallway in the absence of experiments, 0 km/h; temperature 15-24°C; relative humidity, 20-37%; barometric pressure, 29-30 inches of mercury (736.6-762 mm of mercury)]. The experimental setup included two tables, the smaller on top of the larger, upon which a metal stand, a ring, and clamps holding a two speed (slow and fast, no heat) hair blower were positioned at 190.5 cm (75 inches) - a height chosen for safety reasons - above the ground (Figure 3A).

Figure 3. Experimental setup for the airborne time and dispersal distance of *Cercis canadensis* and *Asclepias subulata*. A. Overall setup. Note the narrower exit neck of the funnel used for *C. canadensis* seedpods. B. Closeup of setup used for *A. subulata*.

The wind speed was measured with a digital anemometer (Kestrel 3000 Pocket Weather Meter, Nielsen-Kellerman, Inc., Boothwyn, Pennsylvania, USA). A kitchen funnel was placed directly in front of a hair blower [Vidal Sassoon Ionizer™ hair blower (Vidal Sassoon, China) with the ionizer setting on], which had a PVC pipe (72 mm long, inner diameter 60 mm) attached to its front to concentrate the turbulent air being blown. Dispersules were dropped into the funnel one by one.

Airborne time experiments. We compared the airborne time of ten randomly selected and enumerated *C. canadensis* seedpods and ten *A. subulata* seeds. We repeated this experiment at three different wind speeds (0 km/h, 25 km/h and 35 km/h) always using the same twenty dispersules. A web chronometer (http://online-stopwatch.chronme.com/) was used to measure the travel time. The wider exit neck (Figure 3B) was used for seeds of *A. subulata* to ease their descent.

Distance travelled by Cercis canadensis seedpods experiments. We measured the distance traveled by the 60 enumerated seedpods *C. canadensis*, which were dropped one by one into the funnel on each experiment, experienced a pulse of air immediately upon exiting the funnel (Figure 3A). The hair blower was kept in the on position for approximately two to three minutes, which was the duration of each replicate for every experiment. The horizontal distance travelled by the seedpods of *C. canadensis* with respect to the vertically projected funnel's exit was measured. The middle of the seedpods *C. canadensis* was used as the measuring point. Five different wind speeds[5] (0, 5, 15, 25, and 35 km/h) were tested. Three replicates were performed for each of the eastern redbud seedpods. The experiments wind speed of 5 km/h and 15 km/h required additional adjustments consisting of rods supporting the funnel placed in front of the hair blower at the appropriate distances.

Statistical analyses. For the airborne time experiments, we performed t-tests for every speed tested as well as a two-factor analysis of variance (ANOVA) with replication. The two factors analyzed were, first, species (*A. subulata* and *C. canadensis*) and, second, wind speed. To dissect what may be statistically associated with the large variability in the distance that the dispersules travelled, we performed simple linear regression and two-factor analysis of variance

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[5] Wind speed measurements taken at ground level in a redbud study site are generally about 5 km/h. This study site, which has been visited by author JASB and his collaborators since 2018, is located behind the Nature Center at Nixon Park (latitude 39.8853313, longitude -76.7346893), near the town of Jacobus in York County, Pennsylvania, USA (Frey 2022, Santiago-Blay et al. 2022, Figure 1). This site has about 50 *Cercis canadensis* trees ranging from approximately 3 to 15 m height within an area of approximately 1,000 m^2.

(ANOVA) with replication. In the latter experiments, the factors were, first, wind speed, and second, replicate. Also, we performed multiple regression analyses. Excel was used to complete all statistical analyses. An online site containing the Kolmogorov-Smirnov test (Stangroom, no date) was used to assess the normality of the data distribution for each wind speed - species in the airborne time experiments as well as for each wind speed in the distance travelled by *Cercis canadensis* seedpods experiments. In all cases, the data was not significantly different statistically from that which is normally distributed.

Results

Airborne time experiments. Cercis canadensis seedpods fell to the ground faster than *A. subulata* seeds at every wind speed tested (t-test, $p < 0.001$). Table 1 summarizes our results. These statistical results were supported by a two-factor ANOVA ($p < 0.001$, with speed and species as the two factors) that also strongly suggested that *A. subulata* seeds remain airborne (circa 3.7-3.8 s) longer, approximately 2.75x, than redbud seedpods (circa 1.2-1.5 s).

Table 1. Average time, in seconds (standard deviation) that *Cercis canadensis* seedpods and *Asclepias subulata* seeds take to reach the floor at different wind speeds. Two-factor ANOVA with replication, $p < 0.001$. Under the assumptions of projectile motion, particularly no friction due to air, the expected time of flight with an angle of launch of 0 degrees and an initial height of 1.905 m is 0.623 s (see Appendix 1 and Szyk and Pamula 2023).

	Average time (standard deviation) of dispersule to reach the floor at different wind speeds		
	Wind Speed (km/h)		
Species	0 km/h	25 km/h	35 km/h
Cercis canadensis seedpods	1.27 (0.19)	1.35 (1.30)	1.47 (1.06)
Asclepias subulata seeds	3.75 (1.11)	3.77 (1.18)	3.76 (1.14)

Distance travelled by C. canadensis seedpods. Eastern redbud seedpods dispersed minimally through air (Table 2). Not surprisingly, the higher the wind speed, the more the seedpods disperse (c.f., Figure 4).

Table 2. Average distance travelled, in cm (standard deviation) by *Cercis canadensis* seedpods at different wind speeds, h = 1.905 m.

Wind speed (km/h)	0	5	15	25	35
Average distance travelled, in cm (standard deviation)	38.8 (22.3)	46.9 (24.0)	59.4 (28.5)	78.5 (35.5)	91.7 (42.3)

Although the coefficient of determination, R^2, of the average distance travelled at each wind speed is nearly 0.996 (graph not shown), when the entire data are plotted and the coefficient of determination is recalculated, the R^2 is 0.28, immediately suggesting that factors besides wind speed affect the distance a redbud seedpod travels. A multiple regression model used demonstrates that there is large variation in the distance traveled by the seedpods, with wind speed being the only statistically significant variable among those measured ($p < 0.05$, Table 3).

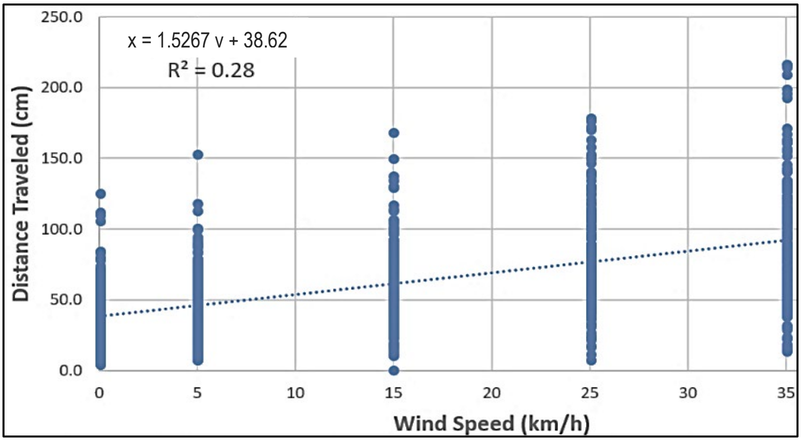

Figure 4. Average distance traveled by *Cercis canadensis* seedpods as a function of wind speed. Note large variation in distance traveled by *C. canadensis* seedpods and the corresponding relatively low coefficient of determination, $R^2 = 0.28$.

Table 3. Summary of the multiple regression analyses conducted on the distance travelled of *Cercis canadensis* seedpods. Wind speed is the only significant ($p < 0.05$) factor related to distance travelled. Significant values are highlighted in slightly larger font and bolded.

Multiple regression analysis						
	df	SS	MS	F	Significance F	
Regression	6	130240.1	21706.69	19.87528859	**1.78385E-19**	
Residual	293	319998.4	1092.145			
Total	299	450238.5				
	Coefficients	Standard error	t Stat	p value	Lower 95%	Upper 95%
Intercept	-561.8264504	455.4762	-1.23349	0.18380717	-1458.246224	334.5933
Seedpod #	0.04510452	0.11621	0.388268	0.698099697	-0.183590837	0.273832
Wind speed	1.574796748	0.14899	10.56981	**2.46429E-22**	1.281570232	1.868023
Mass before	101.8625971	73.16181	1.392292	0.164889783	-42.12668085	245.8519
Area	-0.670715979	0.580521	-1.15537	0.248880631	-1.813235494	0.471804
Pod length	8.031640299	6.91472	1.161528	0.246372626	-5.577174921	21.64046
Pod width	48.83550549	38.01254	1.284721	0.199904505	-25.97671593	123.6477

A two-factor ANOVA with replication not only confirms that there is a statistically significant effect of wind speed ($p < 0.05$, Table 4) on the dispersal of *C. canadensis* seedpods but also a significant interaction effect ($p < 0.05$, Table 4).

Table 4. Summary analyses for a two-factor ANOVA (Analysis of Variance). Wind speed, compared by columns, is significantly ($p < 0.05$) related to distance travelled as is the interaction factor (wind speed and replicate, $p < 0.05$). Significant values are highlighted in slightly larger font and bolded.

Two-factor ANOVA						
Source of variation	SS	df	MS	F	p value	F crit
Sample	194.8583	2	97.42914	0.10102	0.903925	3.005896
Columns	345454.3	4	86363.56	89.54648	6.3E-64	2.38199
Interaction	29367.58	8	3670.948	3.80624	0.000208	1.948848
Within	853542.8	885	964.4552			
Total	1228560	899				

We suggest that this interaction effect on the distance traveled is, in part, related to the precise orientation of the *C. canadensis* seedpods with respect to the pulse of air. We did not control this as the seedpods descended through the funnel (Figure 3B). Furthermore, it was not the purpose of this project to explore the details of the dynamics of the seedpods' movement in the laboratory.

Discussion

We acknowledge the limitations of our experimental method. First, plant dispersules generally do not travel following a projectile trajectory. Based on our field observations, seedpods do not fall following a simple parabolic trajectory (c.f., comments on interaction factor in Table 4). In the forest, as seedpods fall, they may collide with branches and other obstacles on their way down. Second, in a forest, where *C. canadensis* lives, air is not a relatively small, cylindrical moving mass and the fruits are not exposed to just a pulse of air[6]. Instead, wind moves at different velocities through the vertical structures of a forest (Raupach 1994, Finnigan 2000). Third, wind velocity is affected by numerous factors, such as temperature, as well as size, distribution, and density of the obstacles (i.e., as trunk, branches, leaves; Niklas and Spatz 2004, Turner 1988), topography, edge effects (Turner 1988), etc.

[6] Our initial attempts to study how much redbud seedpods move began with fans. However, we quickly realized that we did not have easy access to the appropriate machinery and expertise to simulate nature at an appropriate scale. Hence, we opted for the simpler setup described in the Methods.

In native forests, most seedpods remain attached to the redbud trees and remain closed following abscission. On December 26, 2023, JASB visited the Nixon Park site and walked within and around a cluster of *C. canadensis* trees loaded with thousands of seedpods (Figure 5) finding dozens to hundreds of seedpods under the redbuds' canopy. Also, he found isolated seedpods scattered circa 1-5 meters (circa 3-17 feet) outside the cluster. When JASB vigorously shook several trees, the few seedpods that fell did so vertically or nearly so. In Oklahoma, where *C. canadensis* is the state tree, "a small proportion of the seedpods look like they were opened by insects eating them. Some seedpods were broken off, probably by the wind beating them against the branches. And others were completely burst open - could be due to extreme cold or extreme temperature fluctuation. About 95% of the seedpods were still intact on the tree, not opened. Some seedpods had already fallen to the ground under the tree, but it did not look like the wind had blown them more than a few centimeters (inches) away from the parent tree" (Stoll to Santiago-Blay, personal communication, January 17, 2023). For urban trees, paved surfaces, such as roads, are likely to ease the wind dispersal of *C. canadensis* seedpods and seeds. The same can be said of seedpod dispersal under the influence of extraordinarily strong winds.

Figure 5. A group of redbud trees, *C. canadensis*, loaded with seedpods (brown to dark brown objects on branches) at Nixon Park, York County, Pennsylvania, USA. This has been one of the sites for the study of eastern redbuds that author JASB and colleagues of his have used since 2018.

Based on our field observations as well as those of other colleagues, and our experimental results, we conclude that *C. canadensis* seedpods are minimally dispersed by wind. Houghton et al. (2020) performed similar laboratory experiments on *Astragalus holmgreniorum* Barneby (Fabaceae), a small herbaceous plant, and noted similar limited dispersal. However, unlike their observations, we did not see a single redbud seedpod release seeds as they traveled during our experiments. Also, the seedpod mass of *C. canadensis* decreased only approximately 1% supporting our assertion that redbud seedpods are unlikely to release seeds during their wind-driven sojourns.

If the role of wind dispersal is minimal for *C. canadensis* seedpods, what other evolutionary forces may be responsible for the genetic variation that has been detected within the species?

Dispersal by animals. Animals assist in the admixing of conspecifics through the large geographical range of *C. canadensis* (Sullivan 1994). Some animals (quail, pheasants, and deer, Brown and Brown 1972; birds, Collingwood and Brush 1974; deer, Hunter 1989; eastern woodrats, *Neotoma floridana* (Ord, 1818), Post 1992; deer, cattle, birds, and squirrels, Stubbendieck and Conard 1989) have been reported as herbivores on redbud, and, in some cases, specifically, the seedpods. The bees, *Osmia lignaria lignaria* Say, 1837 (Megachilidae) and *Habropoda laboriosa* (Fabricius, 1804) (Apidae), have been observed carrying pollen of *C. canadensis* (Kraemer et al. 2014, Cane and Payne 1988).

Another source of plant-animal trophic interactions data is the examination of gut contents. In our experience, papers including gut contents data where species identification of the remnants of eaten food items are usually difficult to find. The analyses of digestive tract, including fecal contents, has contributed to the knowledge of animals that feed on *C. canadensis*, including red deer, *Cercus elaphus* Linnaeus, 1758 (Schneider et al. 2006). Those types of data are becoming more accessible owing to advances in molecular genetics and stable isotope techniques (Carreon-Martinez and Heath 2010, Kartzinel et al. 2015, Kundu et al. 2020, Petrone et al. 2023, Rytkönen et al. 2009, Valentini et al. 2009). However, we are unaware of publicly available, searchable, global databases where fecal DNA is identified to species.

Significant genetic (Wadl et al. 2012, Davis et al. 2002, Coşkun 2003, Coşkun and Parks 2009, Thammina et al. 2017 all for congeneric species of *Cercis*; not for genome size and ploidy levels, Roberts and Werner 2016), physiological (Abrams

1988), and morphological (Chen and Werner 2021, Donselman 1976, Donselman and Flint 1982, Roberts et al. 2015) variability has been reported for *C. canadensis*[7].

Selection and genetic drift. On the southern – and more arid - range of its distribution, such as southern Texas (USA) and northern México, some of the variation within redbuds has been linked to environmental factors, such as water availability (Fox et al. 2014, Griffin et al. 2004), suggesting that natural selection is an important evolutionary force shaping the gene pool of *C. canadensis* through its southern range. Conversely, on the northern – and more mesic range - genetic drift via population bottlenecks has been suggested as an ultimate cause of variation on eastern redbuds (Ony 2019, Ony et al. 2019, Ony et al. 2021). As for the time of occurrence of this genetic variation, the possibility that it has an older origin has been suggested (Ony et al. 2021).

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[7] Undoubtedly, *C. canadensis*' genetic variation is being exploited commercially. More than 100 cultivars of this beautiful and economically important ornamental tree are known (Kidwell-Slak and Pooler 2018) and extensive morphological variation has been documented (e.g., flower color, pink is common, variation ranges from white to magenta; leaf color, green is common, variation ranges from yellow – unrelated to the fall – to burgundy), etc. (Roberts et al. 2015, Chen and Werner 2021). Consequently, the species is becoming increasingly planted worldwide (Multiple authors, no date).

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Appendix 1

Under ideal conditions, the coordinates (x, y) of a projectile pushed horizontally with speed, v, from a height, h, are:

$$x = (v)(t),\ y = (½)gt^2 ,$$

where g is the gravitational constant, 9.8 m/s^2. Because t = x/v, eliminating the t yields the following equation,

$$x = (v)\sqrt{\frac{2h}{g}},$$

that describes the horizontal distance the object has moved when it completes its travel, namely, h = 0. A plot of the horizontal distances as a function of air speed is given on Figure 6 (next page).

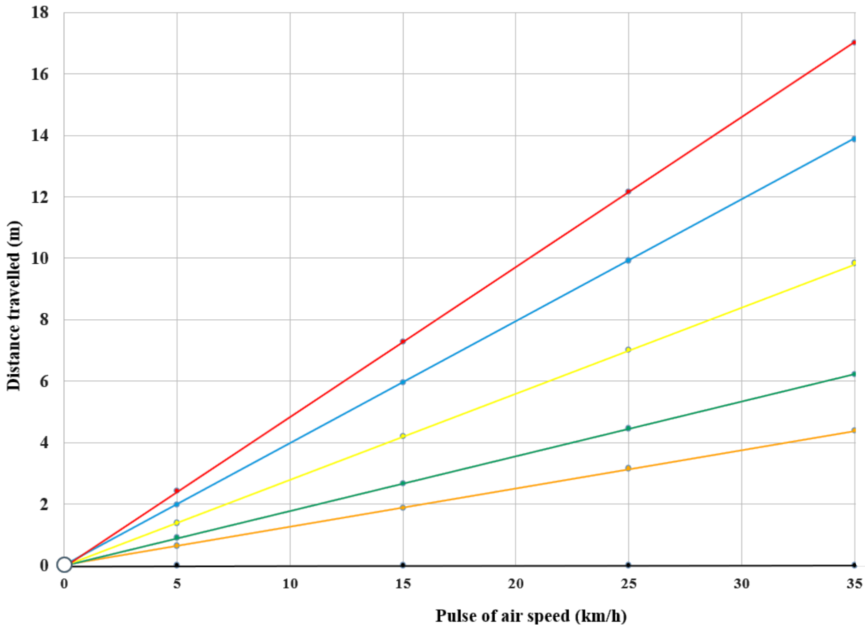

Figure 6. Distance travelled (in m) as a function of pulse of air speed (km/h) under ideal ballistic conditions. Dot's colors denote height (m) from which the object is being propelled: red denotes 15, blue 10, yellow 5, green 2, orange 1, and black 0. The white dot on the origin represents the distance travelled when the pulse of air speed = 0, regardless of the height.