A simple mechanistic model of invasive Heracleum species seeds dispersal by wind (#58509)

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A simple mechanistic model of invasive Heracleum species seeds dispersal by wind

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Background. Invasive species are one of the key elements of human mediated negative ecosystems degradation and ecosystem services impairment worldwide. Dispersal of propagules is the first stage of introduction and the driving force behind biological invasion. The success of biological invasion management directly depend on the the prediction of invasion species ability to spread over long distances. *Heracleum sosnowskyi* is one of the most dangerous invasion species with wind-dispersed seeds in the Eastern Europe. The seeds dispersal by wind was generalized with a number of empirical and mechanistic models of varying complexity. The aim of this work was to develop the simplest possible mechanistic model of *H. sosnowskyi* seed dispersal by wind that allows to determine the dispersal distances with an accuracy comparable to that of empirical measurements.

Methods. We measured and compared the seed traits (terminal velocity, mass, area, wing loading) as well as the release height for *H. sosnowskyi* populations from two geographically distant European Russia regions. We tested two simple mechanistic models: a ballistic model and a wind gradient model using identical artificial seeds with characteristics similar to those of real *H. sosnowskyi* seeds.

Results. The wind gradient model gave the best results. The first calculations of maximum possible seed transfer distances by wind using the model and real weather stations data showed that the role of wind as vector of long-distance dispersal for invasive *Heracleum* species was strongly underestimated. The published dataset with *H. sosnowskyi* seed's traits and release heights allow to model the seed dispersal distances by wind at any geographical point within its entire invasion range using the data from the closest weather stations. Proposed simple model for prediction of *H. sosnowskyi* seeds dispersal by wind may be included in planing processes for management of the species invasion.

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ABSTRACT

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INTRODUCTION

Invasive species are one of key elements of human mediated negative ecosystems degradation and ecosystem services impairment worldwide. Dispersal of propagules is the first stage of introduction and the driving force behind biological invasion (Williamson, 1996; Richardson et al., 2000; Nehrbass et al., 2007). The success and rate of biological invasion directly depend on the mobility of the species, their ability to spread over long distances, the effectiveness of the use of dispersal agents (Pyšek and Richardson, 2007; van Kleunen et al., 2015).

In recent decades, *Heracleum sosnowskyi* Manden. (Apiaceae), an invasive plant species, has attracted considerable attention. Its invasion has significant environmental and socio-economical impact in the Eastern Europe and the European part of Russia (Satsyperova, 1984; Chadin et al., 2017; Ozerova and Krivosheina, 2018; Gudžinskas and Žalneravičius, 2018). The most part of its huge invasion range lies between 48.6°N in the South and 72.6°N in the North. This range occupies territories between 15.0°E on the West and 69.5°E on the East. *H. sosnowskyi* plants do not have any vegetative reproduction structures. The success of the species invasion directly depends on the number of seeds and their ability to dispersal (Dalke et al., 2015; Gudžinskas and Žalneravičius, 2018).

There were several attempts to assess wind dispersal distances of *Heracleum* species seeds. Researchers had made experiments in wind tunnel (Clegg and Grace, 1974) analysis of seedlings density dependence on distance from maternal plant (Pergl et al., 2011), analysis of aerial photographs (Müllerová et al., 2005; Moravcova et al., 2007) and direct measuring of seed flight distance in field conditions (Jongejans et al., 2008; Wojewódzka et al., 2019).

The consensus point of view in literature declare that most of *Heracleum mantegazzianum* (the invasion species that phylogenetically and eco-physiologically is very close to *H. sosnowskyi*) seeds fall not far then 5 m from maternal plants. The dispersal for distances more than 10 meters should be considered as long-distance dispersal (LDD) even for the tallest species of this genus (Pergl et al. 2011). LDD makes a major contribution in the spread of plant species (Nathan and Muller-Landau, 2000). The rate of linear spread found for *H. mantegazzianum* in Czeck Republic was assessed as 10.8 m per year average with maximum 26.7 m per year Müllerová et al. (2005). Many authors declared that the water streams and human activity should play main role in LDD for *H. mantegazzianum*. The water stream may transfer the *H. mantegazzianum* seeds up to hundreds of meters and most seed disperse by water over shorter (less than 40 m) distances (Trottier et al., 2017).

Nevertheless, the wind often is the only dispersal agent for many sites occupied by invasion *Heracleum* species, and we need to re-assess wind as a vector for LDD for these species. We suppose that seed transfer distances by wind may be strongly underestimated because of difficulties in registration of LDD events. The seeds of Apiaceae are adapted precisely for anemochoria. Oval-shaped seeds of *Heracleum* species are flattened, with a wing-like border. Seeds are catapulted from umbels when dry and elastic stems are pushed by wind gusts or moving objects (Levina, 1957; Tackenberg, 2003; Vittoz and Engler, 2007). We found two mentions in literature about LDD by wind for *Heracleum* species up to 100 m for *H. mantegazzianum* (Ochsmann, 2008) and up to 50 m for *H. sosnowskyi* (Kondratiev et al., 2015) although these reports were not confirmed by any instrumental measurements.

The anemochorous seed dispersal is well studied for many plant species and generalized with a number of mechanistic models of varying complexity (Nathan et al. (2011) for review). However, till now none of these models were used for description of seed dispersal of *Heracleum* species.

The aim of this work was to develop the simplest possible mechanistic model that allows to determine the distance of seed dispersal by wind with an accuracy comparable to that of empirical measurements. This model will allow to assess the dispersal kernel and to assess possible events of LDD for different parts of *H. sosnowskyi* invasion range where wind is the only available dispersal agent. This model will allow us to re-assess the significance of wind as an LDD agent for *Heracleum* species and provide practical recommendations for invasion management using weather stations data only.

METHODS

Model Development

The distance of the horizontal flight of propagules in the air flow is known to depend mainly on three parameters: terminal velocity, release height of the seeds and mean horizontal wind speed (Levin et al., 2003; Dauer et al., 2006; Jongejans et al., 2008; Nathan et al., 2011). The simplest mechanistic model of seed dispersal by wind is a simple ballistic model suggested by Dingler (Dingler 1889; cited by Nathan et al. (2011)) and formalized as an equation by Schmidt at the beginning of the 20th century (Nathan et al., 2011):

$$D = \frac{h_r \bar{u}}{V_t} \tag{1}$$

where D is the distance of horizontal flight, $\bar{u}$ is the mean horizontal wind speed, h_r is the seed release height, and V_t is the terminal velocity (constant velocity of seed falling in still air).

The simple ballistic model assumes several simplifications: 1) the seed reaches terminal velocity immediately after release, 2) the horizontal speed of the seed is equal to the horizontal speed of the air flow, 3) the wind does not change speed in the vertical direction, 4) there is no turbulence, and 5) the air flow does not meet obstacles on its path.

Currently, there are a number of models that omit all these restrictions but lead to a complication of the mathematical apparatus, for example, requiring the use of the Navier-Stokes equations (Nathan et al. (2011) for review). We presume that it is possible to accept most of the restrictions of the simplest ballistic model. Some of these restrictions may be accepted because of *H. sosnowskyi* characteristics and its typical habitats in the invaded area. Other restrictions may be accepted after experimental verification.

The assumption about rapid deceleration of seeds to terminal velocity can be empirically verified by measuring the time of seed falling from various heights. The assumption that there is no significant difference between the horizontal speeds of the wind and the seeds flying in air flow can also be tested experimentally. The air turbulence significantly affects the horizontal flight distance only for seeds with a very low terminal velocity: $0.07 \leq V_t < 0.3$ m / s (Nathan et al., 2011). The air turbulence depends on land surface heterogeneity. Our model only considers dispersal of a single plant in open space in order to accept the assumptions that there is no turbulence and that the air flow is not disrupted by obstacles. The *H. sosnowskyi* invasion range is mainly located on the flatlands. Solitary generative *H. sosnowskyi* plants located at a distance of more than several dozen meters from the monostands or any other high (more than 3–5 m) vegetation are not uncommon there.

The vertical gradient of the horizontal wind speed may be incorporated in a simple ballistic model. One of equations describes the wind gradient phenomena as:

$$v_z = v_g \left(\frac{z}{z_g}\right)^{\alpha} \tag{2}$$

where v_z is the speed of the wind at the height z, vg is the speed of the wind at the height z_g, α is the Hellmann exponential coefficient which represents the degree of surface roughness and air stability Cleveland and Morris (2013). We can rewrite the equation (2) with the notation used for simple ballistic model (1):

$$v_h = v_{hr} \left(\frac{h}{h_r}\right)^{\alpha} \tag{3}$$

were v_h is the speed of the wind at the height h, v_{hr} – is the speed of the wind at the height h_r (release height), α is the Hellmann exponential coefficient.

So the mean horizontal wind speed ($\bar{u}$) from the simple ballistic model may be replaced with continuously changing (decreasing) wind velocity v_h. If we accept the assumption about wind and seed velocities equivalence then the horizontal distance of seed flight may be determined by a definite integral of the wind velocity change rate. The h in equation (3) depends on time:

$$h = v_t t_f - v_t t \tag{4}$$

where h is the height at the moment of time t, t_f is the total time of seed falling form the release height to the ground level; v_t is seed's terminal velocity. Now we can replace h in equation (3) with equation (4) to get the wind velocity change rate $v_h(t)$:

$$v_h(t) = v_{hr} \left(\frac{v_t t_f - v_t t}{h_r}\right)^{\alpha} \tag{5}$$

were v_{hr} – is the speed of the wind at the height hr (release height), h is the height at the moment of time t, t_f is the total time of seed falling from the release height to the ground level; v_t is seed's terminal velocity, α is the Hellmann exponential coefficient. The integration of equation (5) allows us to determine the seed's horizontal flight distance:

$$D = \int_0^{t_f} v_{hr} \left(\frac{v_t t_f - v_t t}{h_r}\right)^{\alpha} \tag{6}$$

Here and further, the model introduced by equation (6) will be referred to as the "gradient model". To test whether the gradient model would sufficiently describe seed dispersal of *H. sosnowskyi*, we collected empirical data from seed release experiments.

Data collection

The characteristics of seeds and release heights were determined for *H. sosnowskyi* plants collected at two geographically distant sites located in two Russia regions. Samples were collected in the Syktyvkar city (Komi Republic, Russia) suburbs in 2018 (the North Group) and in the vicinity of Kazan city (Republic of Tatarstan, Russia) in 2017–2018 (the South Group). The North Group plants were from two sites with coordinates: 61.6480°N, 50.7380°E and 61.70°N, 50.80°E. The South Group plants were from two sites with coordinates: 55.80°N, 49.16°E and 55.94°N, 49.27°E. The seeds were collected from and measurements were made in typical monostands of the species. The heights of the central and lateral umbels were measured as the distance from root-stem junction to the top of the main or lateral shoots of the plant.

The seeds were randomly selected from the bulk samples collected in the field. The air-dry weight of seeds was determined using analytical balances with an accuracy of 0.0001 g. To measure the surface area of the seeds (the area of one side), the images of the seeds were obtained using a flatbed scanner at a resolution of 600 dpi. The area of seed images was determined using ImageJ (Schneider et al., 2012).

Wing loading (WL, g / cm^2) was calculated as the ratio of the seed mass (g) to the area of one of its sides (cm^2). The seed falling velocity (V_t, m / s) was determined by measuring the time of falling (t, s) from different release heights (h, m). The measurements were carried out indoors in the absence of air flow at room temperature. Propagules were dropped from heights between 0.80 and 4.28 m. The moment of seed's landing on the floor was visually recorded. The falling time was measured using stopwatches. Each seed was dropped five times and median values were used for subsequent calculations. The North Group of seeds consisted of 70 seeds; the South group consisted of 60 seeds.

It was impossible to find several hundred seeds of *H. sosnowskyi* with the same standard area and mass. Therefore, we used artificial models of *H. sosnowskyi* seeds made of paper, the density of which was close to the average density of seeds of this species in the air-dry state. The contours of the artificial seeds were drawn as ellipses with a major axis of 1.35 cm, a minor axis of 0.88 cm (Fig. 1 B).

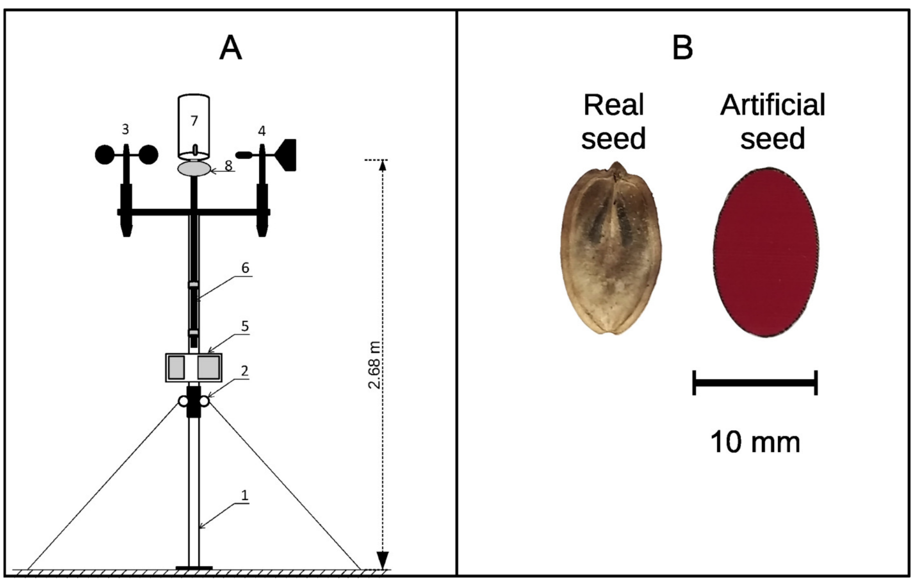

Figure 1. A) Scheme of device for seeds dispersal measuring: 1 – two-section support rod, 2 – rings for struts and fixing the rod, 3 – anemometer, 4 – weather-vane, 5 – data recording block, 6 – removable rod for attaching the container with seeds, 7 – container with seeds, 8 – container cover with a lock for remote seeds release. B) Photo of real *Heracleum sosnowskyi* seed and artificial seed used for model testing.

The traits of artificial propagules were as follows (median values and interquartile range, N=36): mass, 21.5 ± 0.5 mg; area, 0.966 ± 0.018 cm^2; wing loading, 0.022 ± 0.000 g/cm^2. The median terminal velocity measured from a release height of 4.15 m was 1.72 ± 0.11 m/s (N = 10). We conducted all field measurements with these artificial seeds. The main difference between natural and artificial seeds is surface structure. The artificial seeds surface are much smoother and this may influence the air drag force. So, the difference between horizontal wind velocity and seed velocity may be slightly bigger for artificial seeds and distances we observed may be slightly shorter for these seeds than for natural seeds.

The launch of artificial seeds was carried out in natural conditions using a specially designed and manufactured device (Fig. 1 A).

Measurements of horizontal flight distances of artificial seeds were carried out in batches of 10-20 seeds. A batch of seeds was loaded into the container and dropped simultaneously. The wind speed was recorded by videotaping of anemometer readings. The horizontal flight distance of seeds was measured using surveying tape with an accuracy of 0.01 m. Measurements were performed on 26.01.2020, 11.02.2020, 12.02.2020, and 17.02.2020 during daylight hours (11:00 h -16:00 h) in Syktyvkar. As a result, 37 launches of batches of paper ”diasporas” of *H. sosnowskyi* were performed at wind speeds from 0 to 9 m/s.

We conducted all data analysis in R (www.R-project.org). The primary data and R-script used for performing calculations are available at the Zenodo repository (https://doi.org/10.5281/zenodo.3837647).

RESULTS

The correlation between falling velocity and other *H. sosnowskyi* seed traits was measured with North Group only. The North Group seeds were collected at two sites 7.9 km apart. The two samples were combined into one sample according to the Kolmogorov-Smirnov Test (p-value = 0.97 for seed mass, p-value = 0.61 for seed area). The median mass of *H. sosnowskyi* air-dry seeds of the North Group was 11 $\pm$ 3 mg; the median area of one seed was 0.6 $\pm$ 0.2 cm^2; the median value of the wing loading was 0.019 $\pm$ 0.005 g / cm^2; and the median speed of its fall from a height of 2.7 m was 1.62 $\pm$ 0.27 m/s (Table 1).

Summary results	Mass, mg	Area, cm^2	Wing loading, g / cm^2	Falling velocity[a], m / s
Mean	11	0.57	0.019	1.59
Median	11	0.56	0.019	1.62
Standard deviation	4	0.12	0.006	0.25
IQR	3	0.17	0.005	0.27

Table 1. Traits of *Heracleum sosnowskyi* seeds (North Group, n =70).

[a]The falling velocity was determined for a release height of 2.68 m.

The falling velocity depended on the seed mass and the seed wing loading. The most important parameter of *H. sosnowskyi* seeds that affects their terminal velocity is the wing loading coefficient. A linear regression showed that this parameter is responsible for more than 80% of the terminal velocity variability. For a rough estimate of the terminal speed, one can use the seed mass, the fluctuations of which are responsible for about 50% of the terminal velocity variability (Fig.2).

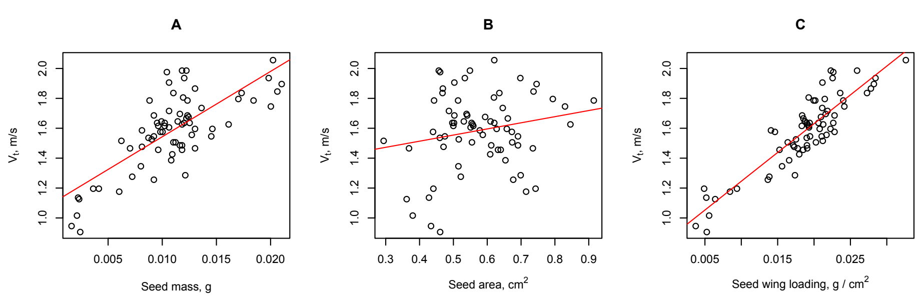

Figure 2. Relationships between *H. sosnowskyi* seed‘s terminal velocity and its mass (A), its area (B) and its wing loading (C). The terminal velocity was determined for a release height of 2.68 m. Linear regression is indicated by a red line. The summary results of the linear regression: A) N = 70, F(1.68) = 88.37, p-value ¡ 0.001, R^2 = 0.57, seed mass = 43.73 $\pm$ 4.65 (p-value $<$ 0.001), Intercept = 1.11 $\pm$ 0.05 (p-value ¡ 0.001); B) N = 70, F(1.68) = 2.78, p-value = 0.10, R^2 = 0.04; C) N = 70, F(1.68) = 277.17, p-value $<$ 0.001 R^2 = 0.80, wing loading = 38.52 $\pm$ 2.31 (p-value ¡ 0.001), Intercept = 0.86 $\pm$ 0.0.05 (p-value $<$ 0.001).

To determine the relationship between the measured mean falling speed in still air and the release height, the seeds were dropped from heights varying from 0.80 m to 4.28 m. Theoretically, as the release height increases, the measured fall rate should approach the terminal (constant) value. Two groups of seeds that differed in wing loading (WL) by more than 3 times were selected for measurements. The seeds of Group A had an abnormally low wing load: N = 4, $WL = 0.006 \pm 0.001$ g / cm^2, 18 measurements of falling velocity. The seeds of Group B had a normal wing load: N = 7, $WL = 0.021 \pm 0.002$ g / cm^2, 42 measurements of falling velocity. The results of linear regression showed that in the used range of release heights it was not possible to determine the relationship between the measured mean fall rate and the release height (Fig. 3). *H. sosnowskyi* seeds reach the terminal speed very quickly and we can adopt the assumption of the simple ballistic model that the seed reaches the terminal speed immediately after its release from the plant.

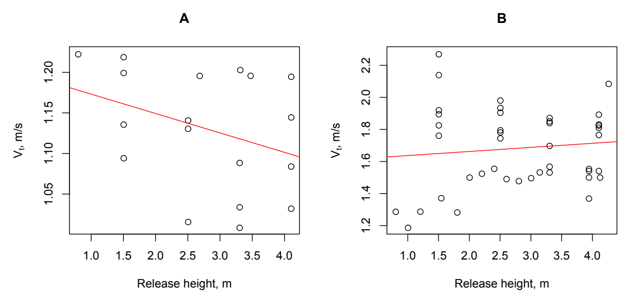

Figure 3. Relationship between *H. sosnowskyi* seed's terminal velocity and release height. A) Seeds with a wing loading of 0.006 ± 0.001 g / cm^2, B) seeds with a wing loading of 0.021 ± 0.002 g / cm^2. Linear regression is indicated by a red line. The results of the linear regression: A) N = 18, F(1,16) = 2.19, p = 0.16, $R^2 = 0.12$; B) N = 42, F(1,40) = 0.47, p = 0.50, $R^2 = -0.01$.

Next, we tested the hypothesis that climate influences the *H. sosnowskyi* seed's characteristics and the release height (the height of umbels above ground level). We compared these characteristics for plants collected in two geographically distant regions: city of Syktyvkar (North Group) and city of Kazan (South Group) located approximately 6°latitude apart. Despite some differences between the traits of North and South plants groups their traits that directly affect the seeds flight distance can be considered almost identical with Kruskal-Wallis test p-value ≥ 0.04 (Fig. 4).

We performed 37 launches of paper seed batches and 414 measurements of the horizontal seed flight distance (8–20 measurements per launch). The wind speeds were between 0 and 9 m / s. Hereinafter in the section "Results", the word "seeds" refers to artificial seed models made of paper, with standard shape and wing loading. An initial analysis of field measurements showed two key features of the relationships between wind speed and distance of horizontal flight (Fig. 5).

First, the distance of the seed's flight strongly correlates with the wind speed (Pearson correlation coefficient is 0.78, p-value $< 2.2 \cdot 10^{-16}$). Second, uniform in shape, weight and size seeds, when dropped simultaneously from the same height, fly off at different distances. With wind speed increasing, the range increased as well. A positive significant correlation was observed between the values of the interquartile range of the flight distances of standardized seeds and the wind speed (Pearson correlation coefficient is 0.74, p-value $< 1.4 \cdot 10^{-7}$). The results of modeling this relationship using a linear regression will be shown below.

We aggregated our empirical data for further analysis. We calculated the minimum (D_{min}), median (D_{median}), mean (D_{mean}) and maximum (D_{max}) seed flight distances for each launch and correlated them with aggregated wind speed measurements: median (vmedian), average (vmean), and maximum (vmax). The highest Pearson correlation coefficient (0.901, p-value $< 2.9 \cdot 10^{-14}$) was obtained for vmax and (D_{mean}). In further analysis, we used this pair of vectors.

Linear regression of the horizontal flight distance (D_{mean}) on the wind speed (vmax) showed that more than 80% of the D_{mean} variability is due to variability of v_{max} (Fig. 6).

We calculated the theoretical horizontal flight distance of seeds using a simple ballistic model at the wind speeds (v_{max}) that we recorded during field experiments and compared them with empirical data using the Kolmogorov-Smirnov test and linear regression (Fig. 7 A1, B1). The simple ballistic model proved to be essentially working: the range of distances obtained as a result of calculations using the

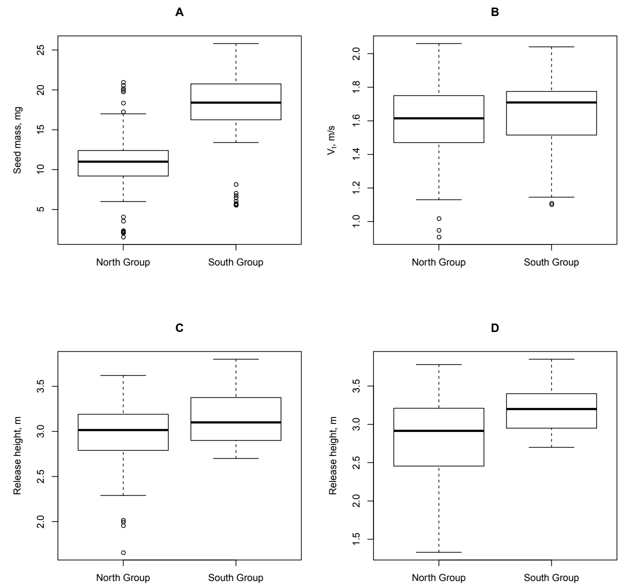

Figure 4. Characteristics of seeds and release heights of *H. sosnowskyi* from two geographically distant regions. North Group – plants collected in the vicinity of Syktyvkar. South Group – plants collected in the vicinity of Kazan. A) seed mass, B) terminal velocity, C) height of the central umbels above ground level, D) height of the lateral umbels above ground level.

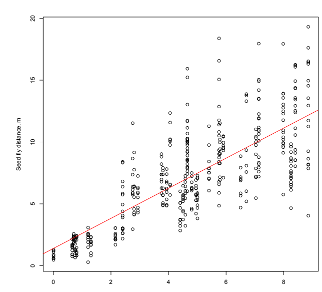

Figure 5. Raw results of measuring the flight distances of artificial *H. sosnowskyi* seeds for different wind speeds. Linear regression is indicated by a red line. Results of linear regression (red line): N = 414, F(1,412) = 604.70, p-value $<$ 0.001, R2 = 0.59, wind speed = 1.22 $\pm$ 0.05 for p-value $<$ 0.001, Intercept = 1.40 $\pm$ 0.26 p-value $<$ 0.001).

equation (1) did not differ significantly from the empirical data (Kolmogorov-Smirnov test: p-value = 0.52). This model allowed us to explain 80% of the variability of experimental D_{mean} values. A significant shortcoming of the simple ballistic model is that the angle of the regression line reflecting the relationship between the calculated and experimental data differed from 45% (tangent = 1) and it's tangent was equal to 0.77 $\pm$ 0.07.

The gradient model allowed us to take into account the vertical wind speed fluctuations by using the ground surface roughness Hellmann exponent (α). We used the same empirical data about wind speed (v_{max}) as for simulation of seed flight distance by the simple ballistic model. To find the coefficient α at which the regression line angle tangent between the calculated and empirical distances is equal to 1.00, we performed a series of the seed flight distance calculations using the gradient model and changing the coefficient α from 0.05 to 0.50 with increment of 0.01. The value of α = 0.29 provided the optimal convergence of the calculated and empirical data (Fig. 7 A2, B2).

As shown above (Fig. 5), empirical data demonstrate that the seed flight distance variation increases as the wind speed increases. The range between the minimum and maximum flight distances of artificial seeds during the same launch linearly depended on the wind speed and ranged from 0.75 m at zero wind speed to 5.27 m at a wind speed of 8–9 m / s. We divided the distance measurement results into classes

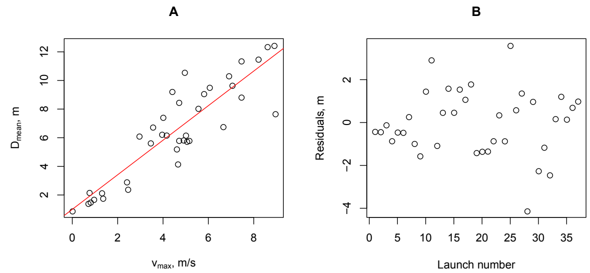

Figure 6. The relationship between the mean flight distance and the maximum wind speed (A), the regression residuals (B). Linear regression is indicated by a red line. Summary of linear regression results: N = 37, F(1,35) = 151.13, p-value < 0.001, R^2 = 0.81, vmax = 1.21 ± 0.10 (p-value < 0.0001), Intercept = 1.05 ± 0.51 (p-value = 0.05).

according to wind speed (v_{max}) and discreditize them with increment of 1 m, then calculated the standard deviation of the seed distance flight (D_{sd}) for each wind speed class. The results of linear regression of D_{sd} on v_{max} showed a strong relationship between these parameters (R^2 = 0.82, p-value = $4.13 \cdot 10^{-7}$). The linear regression equation is:

$$D_{sd} = 0.35 \pm 0.06v + 0.51 \pm 0.29 \quad (7)$$

where D_{sd} is the standard deviation of flight distances of seeds released at the wind speed v. It should be taken into account that there were only nine pairs of vmax and Dsd because of the data discretization. The limited number of pairs did not allow to calculate statistically significant intercept (0.51 ± 0.29, p-value = 0.07) (see primary data and R-script at https://doi.org/10.5281/zenodo.3837647).

DISCUSSION

Simple mechanistic models with three main independent variables (wind speed, terminal velocity and release height) demonstrated a reasonable prognostic accuracy for horizontal flight distances of *H. sosnowskyi* seeds. The comparison results showed that making the simple ballistic model more complex by adding a new parameter α (Hellmann exponent) is adequate. This parameter allowed us to account for a decrease in the wind speed in the vertical direction. Tangent of regression line angle between the calculated and empirical distances became equal to 1 with the optimal value of $\alpha = 0.29$. These Hellmann exponent values correspond well to values recommended for "unstable air above human inhabited areas" ($\alpha = 0.27$) and "neutral air above human inhabited areas" ($\alpha = 0.34$) (Cleveland and Morris, 2013).

Despite the availability of well elaborated mechanistic models for seeds dispersal by wind till now researchers hadn't used them for *Heracleum* species. We can explain this phenomena by difficulties of these models testing by empirical dispersal distance measurement. You need to have hundreds of seeds with identical terminal velocity to make enough replicates of measurements. You cannot use the same seeds for repeated measurements: the wing-like border of seed is very fragile and can be easily broken after the first flight distance measuring cycle. We may declare that using artificial seeds with standard shape, wing loading and terminal velocity close to the corresponding median values of natural seeds allowed us to omit these difficulties.

It was unexpected to reveal a significant difference in flight distance of these artificial seeds after simultaneous drop from the same height under the same wind condition. These differences are probably due to the aerodynamic properties of *H. sosnowskyi* seeds. Nearly oval seeds of the species have a strongly flattened shape, do not have special accessories for aerodynamic stability (wings, pappus) and the center of mass is close to the geometrical center of seed. But this fuzziness can be taken into account and introduced into our mechanistic gradient model using equation (7).

With the developed gradient model and weather stations data we can assess the expected maximum *H. sosnowskyi* seeds dispersal distance. The maximum recorded wind speed for Syktyvkar and for Kazan airports weather stations was 25 m / s at height 10 m. Maximum release height registered by us was 3.85 m.

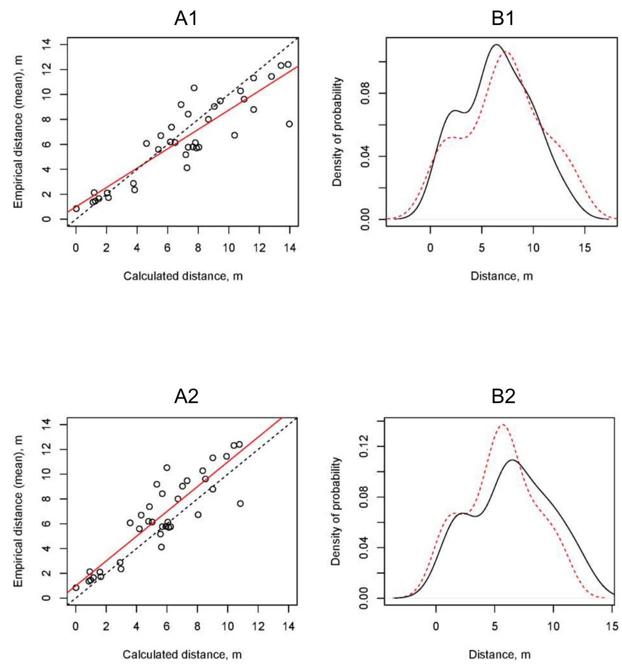

Figure 7. Relationship between empirical seed flight distances and flight distances calculated using the simple ballistic model (upper two plots) and the gradient model with $\alpha = 0.29$ (lower two plots).
A) Results of linear regression (red line), dotted line is 1:1 line:
A1) Dmean = 0.77 ± 0.07 (p-value < 0.001), Intercept = 1.00 ± 0.53 (p-value = 0.07),
A2) Dmean = 1.00 ± 0.09 (p-value < 0.001), Intercept = 1.00 ± 0.53 (p-value = 0.07).
B) Kernel density estimation of empirical seed flight distances (black line) and that of simulated distances (red line). The results of the two-way Kolmogorov-Smirnov test showed that two samples in both cases belong to the same statistical population:
B1) p-value = 0.52,
B2) p-value = 0.35.

We can expect at the height 3.85 m the wind speed 25 m / s measured at height 10 m should be decreased to 17.6 m / s due to wind gradient. The slowest terminal velocity, registered for real *H. sosnowskyi* seeds, was 0.91 m / s. Then the expected dispersal distance for such seeds should be 58 ± 7 m. For the seeds with median terminal velocity (1.65 m / s) the expected dispersal distance should be 32 ± 7 m.

These draft calculations show that one should not exclude wind from the list of LDD agents for *Heracleum* species. The proposed mechanistic model can explain published observations on invasion spread rate (up to 26.7 per year) of *H. mantegazzianum* and individual observations of *H. sosnowsky* seeds extreme flight distances (up to 50 meters).

The *H. sosnowskyi* seed's traits and release heights remain relatively uniform over large geographical areas. The observed differences in terminal velocities and release heights are not sufficient to significantly affect the horizontal flight range of the seeds. The dataset with *H. sosnowskyi* seed's traits (measurements for 130 seeds) and release heights (290 measurements) published in Zenodo (https://doi.org/10.5281/zenodo.3837647) allow to model the seed dispersal distances by wind over its entire invasion range. The only data one needs to add for modeling of seed dispersal by wind in the specific part of the invasion range is the data from closest weather stations.

Within one population, *H. sosnowsky*i seeds may have significant differences in terminal velocity and may be located at different heights above ground level. These differences can lead to significant differences in seed's dispersal by air flow. Therefore, to calculate the entire range of distances of seed's dispersal using the proposed mechanistic gradient model, it is necessary to develop an individual-based model (IBM), in which the flight of each seed is calculated separately. The values of the *H. sosnowsky*i seed terminal velocity and release heights should be selected randomly from a variety of empirically obtained data. Wind speeds for a specific area should be taken for the period from the beginning of seed maturation until the moment when all seeds capable of releasing run out.

Our observations showed that the seeds of *H. sosnowsky*i have very different capacities of releasing from the elements of the inflorescence: some seeds fall off at the slightest vibration of the plant shoot at almost zero wind speed, and some remain on the umbels even after strong gusts of wind exceeding 15 m / s. The dragging of individual seeds or umbrellas with the remaining seeds over the surface of snow by wind requires additional studies. To model the flight distances of seeds released from umbels, it is important to consider that different groups of seeds in the same umbel may have their own critical wind speeds. A critical wind speed is the minimum wind speed at which, and only at which, the seed is released from the umbel.

An important requirement for obtaining adequate results using IBM is the availability of high-quality measurements of the wind speed for a given area performed with the highest possible frequency. The most appropriate information for our purposes is provided by airport weather stations. The weather stations measure the wind speed every 30 min and the information about the maximum wind gusts between measurement periods is also available.

CONCLUSION

Our first results showed that the wind contribution to seed dispersal of invasive *Heracleum* species was strongly underestimated in most studies. More detailed results will be available after the individual based model development. It will allow us to calculate the flight distances of *H. sosnowskyi* propagules, taking into account real weather conditions in different years in different parts of its invasion range. We will describe the direction and dynamics of *H. sosnowskyi* expansion on the unoccupied territories and provide practical recommendations for its invasion management.

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