Flying seeds

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Quick Guide on Plant Seed Aerodynamics

What do we mean by seed dispersal by flying? One of the most common seed dispersal mechanism is through flying, sometimes by exploiting the wind as an additional driving force. Seeds taking off from some height from the ground can trade their potential energy to overcome the aerodynamic resistance of flying over an horizontal distance. This is efficiently done by gliding such as, for example, Alsomitra macrocarpa. Alternatively, seeds might fall as slowly as possible and let the horizontal wind to displace them. The dispersal can be dramatically enhanced by *updrafts*, which are the upward turbulent air currents of the atmospheric boundary layer. Updrafts can lift seeds by hundreds of metres, where the horizontal wind speed is higher and can disperse seeds by hundreds of kilometres (Tackenberg *et al.*, 2003; Nathan *et al.*, 2011). This exceptional dispersal mechanism is known as *long distance dispersal*.

What is a dispersal model? In the first approximation, let us consider steady conditions, viz. we assume that the falling speed and of the wind are constant over time. We neglect the initial transient condition, where the seed accelerates from rest, and the time varying velocity fluctuations due to flight instabilities and wind gusts. Consider a seed falling from a height H at a vertical velocity V in a horizontal wind speed U, where U and V and averaged over the height H. The seed takes a period of time $T = H/V$ to fall, during which it is displaced by a distance $D = TU = HU/V$ (Dingler, 1889; Schmidt, 1918). This simple dispersal model is known as *ballistic* and the vertical velocity V can be approximated with the experimentally measurable mean *terminal velocity* reached by the seed after the initial transient, when dropped in quiescent air. It should be noted, however, that the time-averaged horizontal wind speed decreases approaching the ground with the power of ca. $1/5$, and thus U is typically small even in a considerable breeze. For example, the wind velocity averaged over the lowest 20 cm from the ground is about 8% of the velocity at 10 m height.

Which is the expected terminal velocity?

Figure 1 shows four examples of dispersal units (DU), each comprising the seed and everything it falls with. The mass of these four DU spans over almost three orders of magnitude (Table 1): Taraxacum officinale (0.6 mg), Acer palmatum (42 mg), Zelkova abelicea (67 mg) and Alsomitra macrocarpa (212 mg).

Under the same steady assumptions as above, the vertical component of the aerodynamic resistance (R) is equal in magnitude and opposite in sign to the weigh (W), which is the product of the mass (m) and the gravity acceleration (g): $R = -W = -mg$. Hence, the aerodynamic resistance is known a-priori and it is proportional to the mass. We infer that, for the four DU here considered, also the resistance spans over three orders of magnitude. Surprisingly, though, Table 1 shows that the four terminal velocities are relatively similar, ranging only from 0.39 ms^{-1} to 1.53 ms^{-1}.

To understand why the range of the terminal velocity is small, consider four spherical droplets of water (which has a comparable density to that of most of DU) each with the mass of one of the four DU. Their radii would span only from 0.5 mm to 4 mm! From experiments on spheres (Roos & Willmarth, 1971), we found that they would fall in air at a terminal velocity from 6 ms^{-1} to 16 ms^{-1} (assuming fully rough hydrodynamic conditions) . Hence there is a factor smaller than three between the slowest and the fastest droplet. The terminal velocity of these droplets would be approximately that of the DU if they had a spherical geometry. The DU, instead, show morphological adaptations that allow a reduction of V between 88% and 97%. They achieve this by developing a *wing* with with a large surface area (A) and minimum weight (W).

Which are example of morphological adaptations? Small DU often adopt a porous wing. The resistance R of a surface decreases slowly as the porosity increases up to a critical level, after which it decreases abruptly (Cummins *et al.*, 2017). This limiting porosity decreases with the ratio between the inertia force that pushes the air through the voids, and the viscous forces that refrains it, i.e. with the *Reynolds number*: $Re = V\sqrt{A}/\nu$, where $\nu \approx 1.5 \times 10^{-5}$ $\mathrm{m^2s^{-1}}$ is the kinematic viscosity in air. Therefore, filamentous wings are suitable only for light DU that fall with a low Re.

The filaments of the Taraxacum officinale, for example, forms a 90% porous circular wing (Cummins *et al.*, 2019). Hence, the effective porous wing has an area (A) that is 10 times larger than the solid surface projected on a horizontal plane (Table 1). Furthermore, the weight of the porous wing is 1/10 of the weight of an impervious disk with the same thickness and area, but it provides more than half of the resistance. The flow through the disk also stabilises the wake, resulting in the formation of a steady *separated vortex ring*. If the porous disk was impervious, the wake and thus the flight would have been unsteady, and probably the terminal velocity would have been higher Field *et al.* (1997).

The DU of the Acer palmatum is 70 times heavier than Taraxacum officinale and thus falls at a higher Re (> 1000), where filamentous wings are no longer efficient. To adapt, it forms a blade that autorotates while falling (Lentink *et al.*, 2009; Lee *et al.*, 2014), effectively making a porous disk. This is known in fluid mechanics as an *actuator disk*. Remarkably, the disk area spanned by the blade has a porosity $\epsilon \approx 90\%$ ($\epsilon = 1 - \sigma$, where σ is the *solidity*) and a resistance of about half of that of the equal size impervious disk; which is the same as for the Taraxacum officinale. Whilst blade is stalled, the R is enhanced by a *leading edge vortex* (Lentink *et al.*, 2009), which is stabilised by the non-inertial acceleration of the rotating blade (Lentink & Dickinson, 2009; Arranz *et al.*, 2018).

A different but equally effective morphological adaptation is that of Zelkova abelicea, whose mass is comparable to that of Acer palmatum. The DU includes dry leafs and the twig (Certini *et al.*, 2020). Because the leafs are impervious, the wake is unstable and the DU falls chaotically. However, the dry leafs are very light: its weight per unit area, i.e the *wing loading* $W/A_s = 1.4$, is about half that of the Acer palmatum. Because the leafs are that light, it can carrying up to four of them to achieve a terminal velocity of only 1.26 $\mathrm{ms^{-1}}$.

The DU of Alsomitra macrocarpa is notably heavier than the previous examples of DU, and thus it would have a higher terminal velocity if it had similar morphological adaptations. Therefore, it grows the largest and lightest wing per unit area, thinner also than the filaments of the Taraxacum officinale (< 10 μm) (Azuma & Okuno, 1987). Such large wings allow sufficient vertical force R to balance the weight even if the wing are at a small angle of attack (20°) with the relative flow velocity (Ennos, 1989). The wing loading and the terminal velocity are similar to those of the Taraxacum officinale, which is more than 300 times lighter. Its sophisticated boomerang-like threedimensional shape is optimised for flight stability and for a compromise between maximum range and endurance. The maximum range allows dispersal even in the absence of wing, while endurance might result in higher dispersal in the case of tail wind (Azuma & Okuno, 1987).

A personal concluding remarks Both range and endurance increase with Re, and we would expect that only the largest DU would adapt to glide. Yet, the Ulmus glabra also disperse by gliding and its mass is as low as 5 mg (Ennos, 1989). This reminds us that our initial simplifying assumptions are inadequate to understand all morphological adaptations, and sometimes aerodynamics itself is insufficient. Indeed, the authors enthusiastically remark the need for transdisciplinary research on, for example, the transient condition before terminal velocity is reached, the unsteady flight in turbulence, and the effect of morphological changes during flight.

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Table 1: Example of dispersal units. Data for columns 2-5 is from, respectively: Cummins *et al.* (2019); Lee *et al.* (2014); Certini *et al.* (2020); Azuma & Okuno (1987)

	Taraxacum officinale	Acer palmatum	Zelkova abelicea	Alsomitra macrocarpa
Mass m (mg)	0.63	42	67	212
Projected area of the solid surface, A_s (cm^2)	0.13	1.5	4.5	60
Effective wing area, A (cm^2)	1.50	12	4.5	60
Terminal velocity, V (ms^{-1})	0.39	1.26	1.53	0.41
Reynolds number, $Re = V\sqrt{A}/\nu$	360	3.3k	3.9k	1.1k

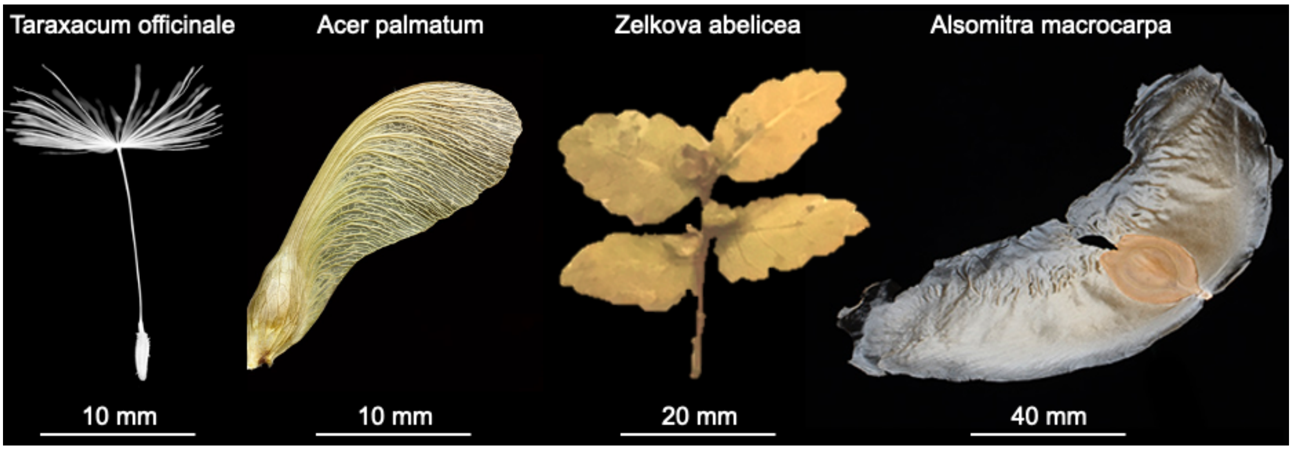

Figure 1: Example of dispersal units.

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