Dandelion Seed Dispersal: The Horizontal Wind Speed Does Not Matter for Long-Distance Dispersal – it is Updraft!

O. Tackenberg, P. Poschlod, and S. Kahmen

Institut für Botanik, Universität Regensburg, Regensburg, Germany

Received: May 22, 2003; Accepted: August 12, 2003

Abstract: **Long-distance dispersal of seeds (LDD) surely affects most ecological and evolutionary processes related to plant species. Hence, numerous attempts to quantify LDD have been made and, especially for wind dispersal, several simulation models have been developed. However, the mechanisms promoting LDD by wind still remain ambiguous and the effects of different weather conditions on LDD, although recognized as important, have only rarely been investigated. Here we examine the influence of wind speed and updrafts on dispersal of dandelion (*Taraxacum officinale* agg.), a typical wind-dispersed herb of open habitats. We used PAPPUS, a weather-sensitive mechanistic simulation model of wind dispersal, which considers frequency distribution of weather conditions during the period the simulation refers to. A simulation for the 4-month shedding period of dandelion shows that high wind speed does not promote LDD. In contrast, vertical turbulence, especially convective updrafts, are of overwhelming importance. Mainly caused by updrafts, in the simulations more than 0.05% of dandelion seeds were dispersed beyond 100 m, a distance commonly used to define LDD. We conclude that long-distance dispersal of seeds of herbaceous species with falling velocities < 0.5 – 1.0 ms^{-1} is mainly caused by convective updrafts.**

Key words: **Seed dispersal, wind dispersal, terminal velocity, Taraxacum officinale.**

The assessment of plant species dispersability is hampered by several problems in measuring dispersal distances, especially when focusing on long-distance dispersal of seeds (LDD), that is dispersal > 100 m (LDD sensu Luftensteiner, 1982; Cain et al., 1998). Hence, simulation models are often used to predict LDD (Clark et al., 1998; Higgins and Richardson, 1999; Bullock and Clarke, 2000; Cain et al., 2000). For wind dispersal, probably the best studied dispersal type, several simulation models have been developed (Schmidt, 1918; Augspurger and Franson, 1987; Greene and Johnson, 1989; Andersen, 1991; Greene and Johnson, 1995; Nathan et al., 2001). However, our knowledge of the mechanisms and conditions promoting LDD by wind is far from satisfying (Horn et al., 2001; Nathan et al., 2002; Tackenberg et al., 2003). Especially the effect of weather conditions on LDD has been investigated only rarely, although weather conditions may considerably effect LDD (Hildebrand, 1873; Nathan et al., 2001; Tackenberg, 2003). For example, Nathan and co-workers (Nathan et al., 2002) have proved only recently a predominant role of updrafts for LDD of tree species with winged seeds. In forests such updrafts are induced mainly by shearing and friction forces, which increase with increasing wind speed (Horn et al., 2001). Hence, Nathan and co-workers argue that LDD of forest trees is not only related to updrafts, but also promoted by high wind speed (see also Nathan et al., 1999).

When focusing on wind dispersal of herbs of open habitats, an important difference to forest species has to be mentioned: In open habitats updrafts are probably mostly caused by convection currents, whereas updrafts caused by shearing and friction forces seem to be less relevant, but this assumption has not been validated by data so far. However, the relative importance of wind speed and updrafts for LDD may differ between open habitats and forests.

Besides these somehow sophisticated differences in the type of updrafts between forest and open habitats, a widespread assumption is that high horizontal wind speeds ("extreme events") also play a dominant role for LDD in open habitats (e.g. Greene and Johnson, 1989; Andersen, 1991; Jongejans and Schippers, 1999; Bullock and Clarke, 2000). On the contrary, a previous study suggests that in open habitats the effect of wind speed on LDD is much smaller than commonly assumed (Tackenberg, 2003). However, this study missed consideration of the frequency distribution of weather conditions during the shedding period. Obviously, the importance of updrafts may be reduced if updrafts occur very rarely during the shedding period. Hence, the main aim of the present study is to assess the relative importance of wind speed and updrafts on LDD for a typical "wind-dispersed" herb species from open habitats under natural meteorological conditions.

We chose dandelion (*Taraxacum officinale* agg.) as the model species. There is one seed per flower, bearing a pappus, which is made up of ca. 0.6 cm long rigid hairs. The pappus serves as a parachute and causes the relatively low falling velocity of about 0.38 m s^{-1} (Tackenberg, 2001). To address intraspecific variation, we assume that the falling velocity of dandelion seeds varies between 0.25 – 0.5 m s^{-1}, which is 30% around the

Plant biol. 5 (2003): 451 – 454

ISSN 1435-8603

mean. Only 2 of 15 analyzed populations (i.e. the populations with the highest and lowest V_{term}, respectively) do not fall into this interval (Table 4 in Tackenberg et al., 2003). The release height ranges from 0.1 to 0.3 m.

Wind dispersal of dandelion is simulated with PAPPUS, a mechanistic wind dispersal model that simulates flight trajectories of individual seeds (Tackenberg, 2003). The model explicitly addresses the effects of weather conditions on wind dispersal and uses measured (instead of simulated) courses of the wind vector. For the simulations, we used horizontal wind speed, wind direction and vertical wind speed measured with a frequency of 10 Hz using an ultrasonic anemometer (USA 1; Metek GmbH, Elmshorn, Germany). A frequency of 10 Hz is necessary to account for the high-frequency fluctuations of the wind vector, which considerably influences the flight trajectory. The anemometer was located in the measurement field of the weather station at Bad Lippspringe (Germany) at a height of 0.7 m. The measurements lasted from May to October 2001, that is the shedding period of dandelion in Central Europe (Müller-Schneider, 1986). Due to some technical problems, the measurements addressed only 2435 h, which are 85% of this period.

For each of the 2435 h we simulated 2000 flights of dandelion seeds, assuming a flat landscape covered by a short-cut meadow, and calculated the proportion of seeds exceeding 100 m distance from those flights. Finally, we calculated the distance spectrum for the whole shedding period by summing the hourly distance spectra.

With multiple linear regression (SPSS 10.0), we tested for the effect of wind speed and updrafts on LDD. Aiming to describe the frequency, strength and duration of updrafts with a single parameter, we developed the parameter "Proportion of LDD-relevant updrafts". Proportion of LDD-relevant updrafts gives the proportion of time within 1 h during which updrafts of a minimum vertical up-wind speed occur. The minimum vertical wind speed is defined by the minimum falling velocity of the seeds (for dandelion = 0.25 m s^{-1}). The time period for which the vertical wind speed is averaged is 100 m divided by the mean horizontal wind speed. Hence, updrafts of that strength and duration are capable of prolonging the flight of a seed such that it may reach 100 m distance without losing altitude in relation to the initial release height (see also Tackenberg, 2003).

Table 1 Effects of LDD-relevant updrafts and wind speed on proportion on LDD. B: regression coefficients, P: significance, T: t-value for B. Linear regression model: df = 2434, F = 3779, R^2 = 0.76, $P < 0.001$; depend variable is proportion of seeds dispersed > 100 m

	B	P	T
Constant	1.5 E-4	0.04	2.9
Proportion of LDD-relevant updrafts	0.51	< 0.001	84.3
Mean wind speed	– 3.4 E-6	0.79	– 0.3

We found that more than 75% of the variation in the proportion of seeds exceeding 100 m can be explained by "Proportion of LDD-relevant updrafts", whereas mean hourly wind speed has no additional explanatory power (Table **1**, see also Fig. **1**). The missing relationship between horizontal wind speed and LDD was surprising only on the first view: Assuming a flat landscape and a non-turbulent flow without up- or downdraft, the best wind-dispersed dandelion seeds (H_{rel} = 0.3 m, V_{term} = 0.25 m/s) stay less more than 1 s in the air. Travelling 100 m in that time span requires a wind speed > 80 m/s (300 km/h). Obviously, such wind speed rarely occurs, at least in the relevant height of dandelion capitula.

We conclude that LDD over the whole shedding period is not promoted by high wind speeds but by convective updrafts. However, according to Fig. **1 B**, LDD sometimes occurs even when the proportion of LDD-relevant updrafts is zero. This is due to the calculation of "Proportion of LDD-relevant updrafts" and not contrary to the importance of updrafts. Even if "Proportion of LDD-relevant updrafts" is zero, there may be up-

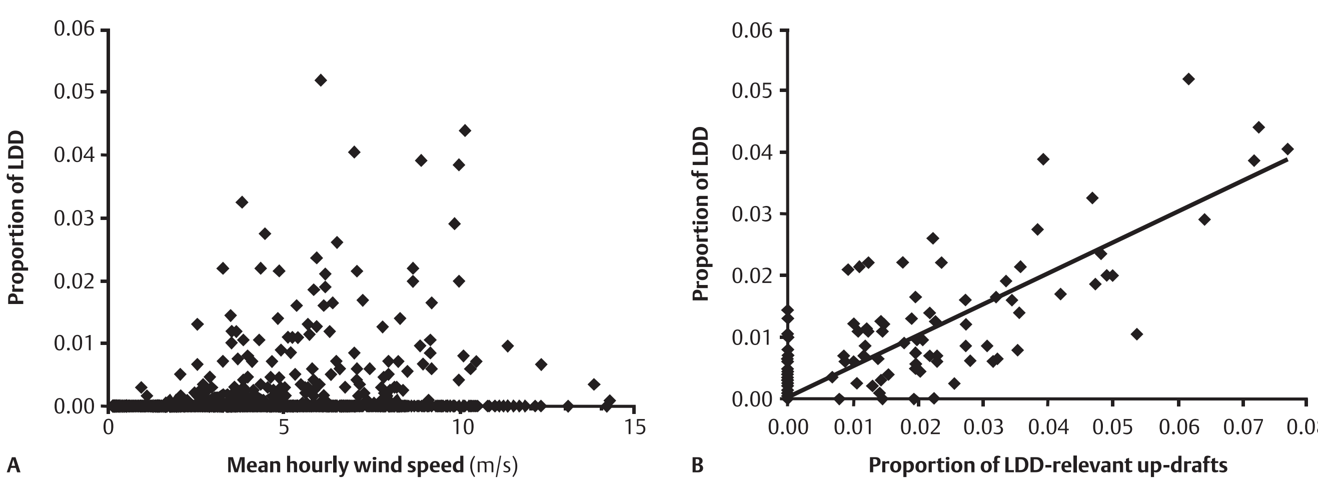

Fig. 1 Relationship between LDD of dandelion and (**A**) horizontal wind speed and (**B**) proportion of LDD-relevant updrafts for 2435 h during the shedding period of dandelion in Bad Lippspringe (Germany) from May to October 2000. Proportion of LDD is the proportion of seeds dispersed > 100 m. Wind speed refers to 10 m height.

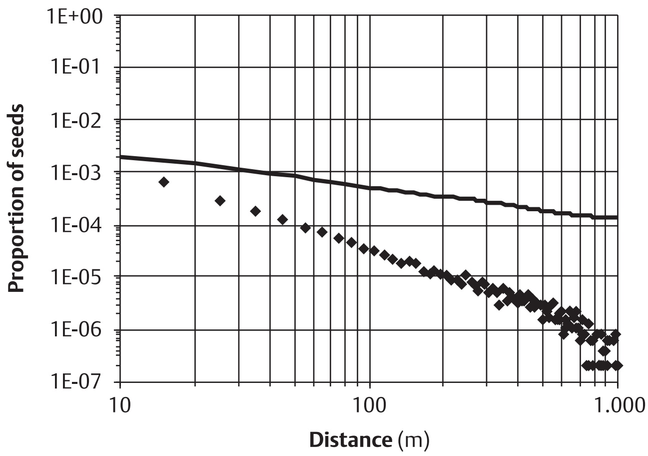

Fig. 2 Dispersal distance spectrum for dandelion. The dots give the proportion of seeds landing in 10 m distance intervals. The line gives the proportion of seeds dispersed beyond the distance on the X axis. The distance spectrum was calculated according to the frequency distribution of weather conditions measured during the shedding period of dandelion in Bad Lippspringe (Germany) from May to October 2000 in a meadow.

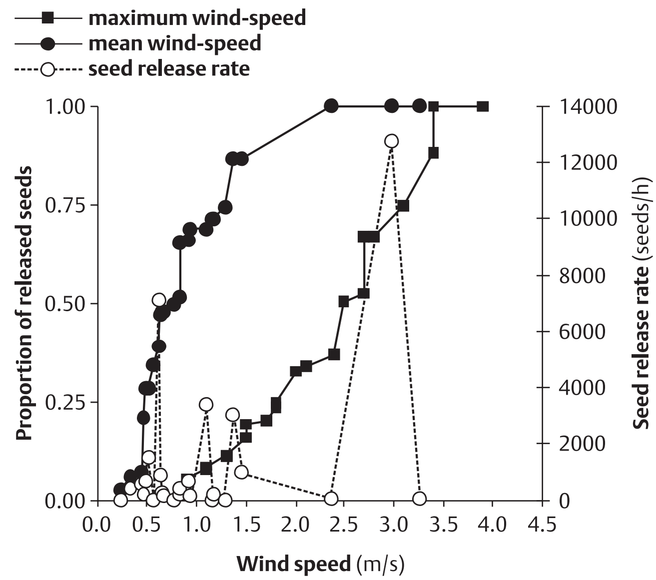

Fig. 3 Seed release rates and sum curves sorted by wind speed for dandelion, based on 25 counting intervals. The proportion of released dandelion seeds is shown in respect to the maximum hourly wind speeds during the interval (quadrats) and in respect to the mean wind speed (circular dots). Seed release rate is pictured only in relation to mean wind speed during the interval.

Table 2 Phenological phase and proportion of released seeds

Phenological phase	Mean proportion of released seeds
No seeds released	0
Few seeds released	0.01
< 10% seeds released	0.05
10 – 50% seeds released	0.3
50 – 75% seeds released	0.625
75 – 90% seeds released	0.875
Few seeds not released	0.99
All seeds released	1

Mean seed production per capitule is 224 (SD = 58, N = 20).

drafts strong enough to prolong the flight of a seed, although the mean vertical wind speed is somewhat weaker than the falling velocity of dandelion seeds (0.25 m s^{-1}).

Finally, we calculated a dispersal distance spectrum for the whole shedding period (Fig. **2**). More than 99.5% of the seeds landed within the first 10 m (not pictured in the graph), 0.05% exceeded 100 m, and 0.014% had the potential to be dispersed > 1 km. At first sight, these proportions seem to be rather low, but calculated for an entire population the absolute numbers might be quite high. We estimated seed production of dandelion on a fertilized meadow of app. 1 ha in size on the campus of the University of Regensburg in 10 regularly distributed quadrats of 2 – 4 m^2. We counted > 70 individuals per square meter (mean = 72, SD = 44, N = 10) and more than 200 seeds per capitulum (mean = 224, SD = 58, N = 20). Hence, one 1-ha meadow population may consist of > 700 000 individuals which produce > 140 000 000 seeds. According to the simulations from this population, > 70 000 seeds would be dispersed beyond 100 m and about 20 000 seeds have the potential to be dispersed > 1 km.

A last process has to be taken into account to finally assess the effect of wind on LDD: seed release may be biased to high wind speeds. A positive effect of high wind speed on seed release seems to occur in many tree species with winged seeds (Kohlermann, 1950; Greene and Johnson, 1992). For herbs, such data hardly exist. In a simple study, we measured seed release and wind conditions in the already mentioned meadow population on the campus of the University of Regensburg. We counted the number of dandelions – 1699 individuals – in different phenological phases (Table **2**) growing in five 2-m^2 quadrats. This was done 25 times during the whole shedding period of this population (29.4. to 24.5.2001), which is on average once a day. From these data we calculated the number of non-released seeds of the 1699 individuals for each counting date using the mean value of 224 seeds per capitule. The number of released seeds between two consecutive counting dates was calculated as the difference between non-released seeds at the two dates. To characterize wind conditions we used hourly wind speeds measured at a nearby meteorological station (Sarching near Regensburg). On the one hand, we used the mean of the hourly wind speeds during two consecutive counting dates, on the other hand the maximum of the hourly wind speeds.

We found that one quarter of the seeds was released during periods with mean hourly wind speeds < 0.5 m s^{-1} and maximum hourly wind speeds < 2.0 m s^{-1} and half of the seeds during time periods with mean hourly wind speed < 0.8 m s^{-1} and a maximum hourly wind speed < 2.5 m s^{-1}. We found no clear trend for higher release rates caused by higher wind speed (Fig. **3**). Although the presented study of seed release is based on only one season and one population, the result strongly indicates that dandelion seeds are released commonly under calm weather conditions. Even under very calm conditions there are gusts present being strong enough to loose the easily detachable seeds from the mother plant. Mayer (2000) even argued that updrafts may be more effective to free *Cirsium arvense* achenes from the capitula than horizontal winds. However, further studies are needed to fully understand the effect of weather conditions on seed release and subsequent dispersal for herbs, as well as for trees.

In conclusion, the overwhelming importance of convective updrafts for LDD can confidently be assigned to all herb species of open habitats, if the falling velocity of their seeds is lower or only slightly higher than that of dandelion. During the shedding period, updrafts that are strong enough to lift seeds with higher falling velocities occur only rarely. However, the strength of updrafts in this study is deduced from measurements in a flat meadow in Central Europe with the strongest measured LDD-relevant updrafts of about 0.5 m s^{-1} during a year. In other vegetation types and landscapes, much stronger updrafts might occur. For example, we frequently measured LDD relevant updrafts > 1.0 m s^{-1} on an alpine glacier foreland. In such habitats, even seeds with relatively high falling velocities might be effectively dispersed by wind. Hence, dispersability should not be deemed as a pure trait of the plant species, as it is also affected by the weather conditions in the respective habitat and landscape.

Acknowledgements

We thank Inge Lauer for the measurement of seed release and seed production. The staff of the weather station at Bad Lippspringe supported the turbulence measurements. Ken Thompson and David Greene commented thoughtfully on the manuscript. The German Ministry for education and research financed parts of this study within the MOSAIK-project (FKZ 01 LN 0007).

References

Andersen, M. (1991) Mechanistic models for the seed shadows of wind-dispersed plants. American Naturalist 137, 476 – 497.

Augspurger, C. K. and Franson, S. E. (1987) Wind dispersal of artifical fruits varying in mass, area, and morphology. Ecology 68, 27 – 42.

Bullock, J. M. and Clarke, R. T. (2000) Long distance seed dispersal by wind: measuring and modelling the tail of the curve. Oecologia 124, 506 – 521.

Cain, M. L., Dammann, H., and Muir, A. (1998) Seed dispersal and the Holocene migration of woodland herbs. Ecological Monographs 68, 325 – 347.

Cain, M. L., Milligan, B. G., and Strand, A. E. (2000) Long-distance seed dispersal in plant populations. American Journal of Botany 87, 1217 – 1227.

Clark, J. S., Fastie, C., Hurtt, G., Jackson, S. T., Johnson, C., King, G. A., Lewis, M., Lynch, J., Pacala, S., Prentice, C. et al. (1998) Reid's Paradox of Rapid Plant Migration. BioScience 48, 13 – 24.

Greene, D. F. and Johnson, E. A. (1989) A model of wind dispersal of winged or plumed seeds. Ecology 70, 339 – 347.

Greene, D. F. and Johnson, E. A. (1992) Fruit abscission in *Acer saccharinum* with reference to seed dispersal. Canadian Journal of Botany 70, 2277 – 2283.

Greene, D. F. and Johnson, E. A. (1995) Long-distance wind dispersal of tree seeds. Canadian Journal of Botany 73, 1036 – 1045.

Higgins, S. I. and Richardson, D. M. (1999) Predicting plant migration rates in a changing world: The role of long-distance dispersal. American Naturalist 153, 464 – 475.

Hildebrand, F. (1873) Die Verbreitungsmittel der Pflanzen. Leipzig: Engelmann, pp. 183.

Horn, H. S., Nathan, R., and Kaplan, N. L. (2001) Long-distance dispersal of tree seeds by wind. Ecological Research 16, 877 – 885.

Jongejans, E. and Schippers, P. (1999) Modeling seed dispersal by wind in herbaceous species. Oikos 87, 362 – 372.

Kohlermann, L. (1950) Untersuchungen über die Windverbreitung der Früchte und Samen mitteleuropäischer Waldbäume. Forstwissenschaftliches Centralblatt 69, 606 – 624.

Luftensteiner, H. W. (1982) Untersuchungen zur Verbreitungsbiologie von Pflanzengemeinschaften an vier Standorten in Niederösterreich. In Bibliotheka Botanica, Stuttgart: Schweizerbartsche Buchhandlung, pp. 68.

Mayer, F. (2000) Long Distance Dispersal of Weed Diaspores in Agricultural Landscapes – The Scheyern Approach, Vol. 47. Aachen: Shaker.

Müller-Schneider, P. (1986) Verbreitungsbiologie der Blütenpflanzen Graubündens. Veröffentlichungen des Geobotanischen Institutes der ETH, Stiftung Rübel 85, pp. 263.

Nathan, R., Katul, G. G., Horn, H. S., Thomas, S. M., Oren, R., Avissar, R., Pacala, S. W., and Levin, S. A. (2002) Mechanisms of long-distance dispersal of seeds by wind. Nature 418, 409 – 413.

Nathan, R., Safriel, U. N., and Noy-Meir, I. (2001) Field validation and sensitivity analysis of a mechanistic model for tree seed dispersal by wind. Ecology 82, 374 – 388.

Nathan, R., Safriel, U. N., Noy-Meir, I., and Schiller, G. (1999) Seed release without fire in *Pinus halepensis,* a Mediterranean serotinous wind-dispersed tree. Journal of Ecology 87, 659 – 669.

Schmidt, W. (1918) Die Verbreitung von Samen und Blütenstaub durch die Luftbewegung. Österreichische Botanische Zeitschrift 67, 313 – 328.

Tackenberg, O. (2001) Methoden zur Bewertung gradueller Unterschiede des Ausbreitungspotentials von Pflanzenarten. – Modellierung des Windausbreitungspotentials und regelbasierte Ableitung des Fernausbreitungspotentials, Vol. 347. Berlin: Cramer, pp. 138.

Tackenberg, O. (2003) Modeling long distance dispersal of plant diaspores by wind. Ecological Monographs 73, 173 – 189.

Tackenberg, O., Poschlod, P., and Bonn, S. (2003) Assessment of wind dispersal potential in plant species. Ecological Monographs 73, 191 – 205.

O. Tackenberg

Institut für Botanik
Universität Regensburg
93040 Regensburg
Germany

E-mail: oliver.tackenberg@biologie.uni-regensburg.de

Section Editor: H. Rennenberg