Take-off in anemochorus dispersal units of Carpinus betulus and Clematis vitalba: Observation in wind tunnel experiments and measurement of the basic force

By

Patrick Fonger and Norbert Pütz

With 2 figures and 1 table

Abstract

FONGER, P. & PÜTZ, N.: Take-off in anemochorus dispersal units of *Carpinus betulus* and *Clematis vitalba:* Observation in wind tunnel experiments and measurement of the basic force. — Bot. Jahrb. Syst. **124**: 105–114. 2002. — ISSN 0006-8152.

Preliminary experiments on dispersal units of *Carpinus betulus* and *Clematis vitalba* were aimed at quantitative measurement of the basic forces involved in take-off. The measurements were completed using the spring scale principle. In *Carpinus betulus*, the take-off force measurements demonstrate that the basic force of take-off correlates to ripeness of dispersal unit. The values for basic force measured were shown to decrease over time, until a minimum take-off force of 0.2 N was finally reached.

The force of dispersal unit take-off for *Clematis vitalba* was also found to be comparable. Several wind tunnel experiments were also carried out with this species. The parameters for take-off were turbulent wind flow and a wind velocity of 17 m/s. Moreover, *C. vitalba* shows individual adaptation under these conditions, with oscillating movements of the branches, and a complete 'shake off' of the dispersal units.

It would appear that these take-off strategies, examples of which are described here, are important in the discussion of dispersal distances.

Keywords: diaspore, dispersal, anemochory, *Carpinus betulus, Clematis vitalba.*

Zusammenfassung. In orientierenden Versuchen wurden bei Diasporen (Ausbreitungs-einheiten) von *Carpinus betulus* und *Clematis vitalba* die Ablösekräfte quantitativ bestimmt. Die Messung der Ablösekräfte erfolgte mit einer Messmethode nach dem Federwaagenprinzip. Die ermittelten Ablösekräfte korrelierten bei *Carpinus betulus* mit dem Reifungsgrad der Diasporen und wurden im Versuchszeitraum geringer, bis schließlich eine minimale Ablösekraft von etwa 0,2 N errreicht wurde. Auch bei *Clematis vitalba* konnte eine notwendige Ablösekraft in vergleichbarer Größenordnung festgestellt werden.

Bei *Clematis vitalba* wurden zudem Windkanalexperimente durchgeführt. Bei turbulenter Windströmung und einer Windgeschwindigkeit von 17 m/s lösten sich alle Diasporen von der Mutterpflanze. Überdies konnte bei *Clematis vitalba* eine individuelle Anpassung konstatiert werden, denn durch Oszillationsbewegungen der Zweige bei turbulenter Windströmung wurden die Diasporen regelrecht abgeschüttelt.

Introduction

Dispersal refers to the transportation of dispersal units (diaspore, "seed", BONN & POSCHLOD 1998). This process is dynamic (CHRISTIANSEN 1954, HECKER 1981). Dispersal is thus one of the mobile phases of plants, and enables plant populations to defend current locations and conquer new habitats (MÜLLER-SCHNEIDER 1983).

In higher plants, anemochorus dispersal is predominant (MÜLLER-SCHNEIDER 1983), and wind properties are thus a key factor. Both dispersal unit take-off (KOHLERMANN 1950) and subsequent movement are impacted by the wind. A connection between wind velocity and dispersal distance has frequently been proven (SHELDON & BURROWS 1973, SHELDON & LAWRENCE 1973, LUFTENSTEINER 1982, AUGSPURGER & FRANSON 1987) by measurements of diaspore sinkage and also wind tunnel experiments (MATLACK 1987, ANDERSEN 1992, 1993, EMIG & LEINS 1994). Most of this experimental work was aimed at finding out dispersal distances. In some cases, the expectation is that dispersal unit take-off takes place at a range of wind velocities (MÜLLER-SCHNEIDER 1983, MÜLLER 1996). However, if viewed as a mechanical process, this suggestion would appear to indicate that dispersal unit take-off requires a range of different forces. Moreover, it can be assumed that there is a connection between the various forces necessary in take-off and the functional strategies which allow dispersal only when natural parameters are favorable.

Up to the present, no approach able to quantify dispersal unit take-off experimentally has been developed. At the same time, various ways of quantification are possible. Firstly, the moment of take-off can be determined in terms of wind velocity, where continuously increasing wind flows impact dispersal units. Secondly, the moment of take-off can be determined in terms of force, where the blowing of the wind is simulated as a pulling force.

Examples of both approaches, i.e. determination in terms of wind velocity, or as a pulling force, are outlined in this paper.

Material and methods

Measurement to the spring scale principle

This method is based on the assumption that the cross-section of the diaspore resists wind. A pulling force on the dispersal unit thus aries (F_{wind}), according to the direction

of the wind. Following take-off, F_{wind} causes dispersal movement. However, dispersal units are attached to the plant. The pulling strength of the tissue at the predetermined breaking point acts like a counter force (F_{tissue}), which may be termed separation resistance ("Abtrennwiderstand", JOHNSON 1988, BONN & POSCHLOD 1998). Our experiments assumed these forces (F_{wind} and F_{tissue}) to be acting in opposite directions (see Fig. 1 A). Take-off occurs when F_{wind} becomes greater than F_{tissue}, and wind flow separates the dispersal units.

In fact, in our measurements the force necessary for take-off was created artificially using a spring scale, the force $F_{springscale}$ thus replacing the force F_{wind} (Fig. 1 B). A spring scale with a range of up to 2 N was used with *Carpinus betulus*. The *Clematis vitalba* measurements were executed using a spring scale of greater sensitivity (range of 1 N, Phywe Düsseldorf). Attached by small clamps, these spring scales were suspended from the highest rungs of a pair of ladders. It was possible to clamp the dispersal unit to the spring scale using a crocodile clip (Conrad Electronic Hirschau, see Fig. 1 B). This crocodile clip was fixed to the force hook of the spring scale by a 5 cm long piece of nylon thread (fishing line, 0.5 mm).

For measurements of *C. betulus* we used dispersal units growing at a height of 3–4 m. For this reason, 20-cm-long tree branches including dispersal units were pruned using a pair of shears. The ripest dispersal units on these branches were chosen (parameters: (1) color: as brown as possible; (2) consistency: as solid as possible). These units were clamped to the apparatus at the position of their nuts. The branch and the dispersal unit under test was then pulled carefully down. With a great enough pulling force ($F_{springscale}$), the dispersal unit came off at the predetermined breaking point. At this point, separation resistance reduced to zero, and the spring scale sprang back to the starting position (= 0 N). Thus, take-off force is that force indicated on the force scale of the spring scale immediately before take-off occurs.
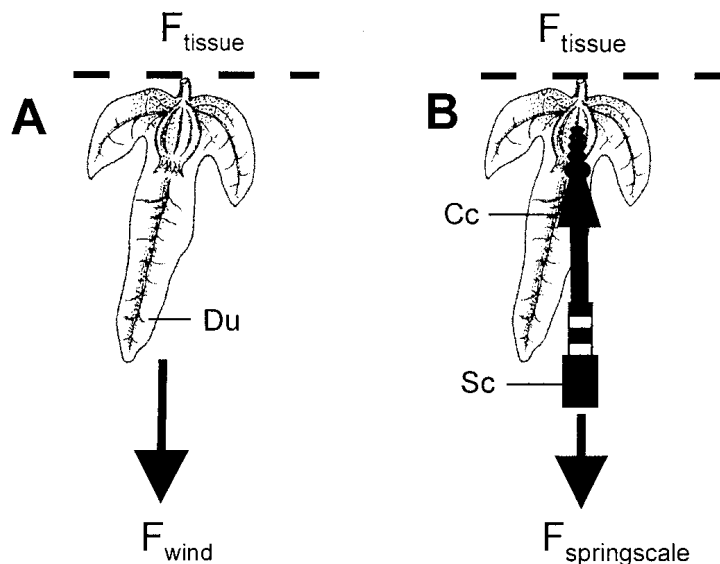

Fig. 1. Basis for the experiments. — A: Balance of forces during wind flow; B: Pulling force of the spring scale in the experiment. — Du = dispersal unit; Cc = Crocodile clip, Sc = Spring scale.

For *Carpinus betulus* L. (Corylaceae) 5 trees were chosen in Aachen-Metalen. 50 dispersal units were measured at two-week intervals. Measurements were started in September and completed mid-December. The mean of each batch of 50 individual measurements was calculated. In addition, calculation of the standard deviation according to BRONSTEIN & SEMENDJAJEW (1991) was completed.

Measurements of the force of take-off of *Clematis vitalba* L. (Ranunculaceae) were carried out in December, in parallel with the wind tunnel experiments. To obtain a mean value, 100 dispersal units were measured. The dispersal units tested grew to a height of 2–4 m.

Wind tunnel experiments

The wind tunnel used has an open 5 m measuring path and a 3 m measuring diameter. In our investigations, we were able to use a blower, producing wind velocities up to 17 m/s (= 61.2 km/h, i.e. a wind force of 7 on the Beaufort scale, i.e. strong winds).

20 branches of *Clematis vitalba* L. (each 20 cm long, and stocked with 25 dispersal units) were fixed into the clamp in succession. This clamp was screwed to a controlling apparatus, which allowed the test objects to be brought into the wind flow. Initially, the response and take-off of the dispersal units were examined in a laminar wind flow. Wind velocity was stepped up gradually from 1 m/sec to 17 m/sec. Next, a turbulent wind flow was produced by stretching out the fingers of a hand, held into the wind flow at a distance of 30 cm from the branch. With this modification, the response of 20 branches (each stocked with 25 dispersal units) was re-measured.

Measurements of fresh and dry weight

After each spring scale measurement, the dispersal units of *Carpinus betulus* tested were individually packet, and the fresh weight examined in the laboratory (analysis scale SBC 32, Scaltec Instruments, Heiligenstadt). After drying at 65°C for 24 h (drying case, Heraeus, Hanau), the dry weight was determined.

The mean and standard deviation values were calculated from these single measurements. In addition, the proportional difference in weight (x_{Diff}) was calculated for each dispersal unit according to the following formula (where x_{Fresh} = fresh weight, and x_{Dry} = dry weight).

$$x_{Diff} = [x_{Fresh} - x_{Dry}) \cdot 100]/x_{Fresh} \qquad (1)$$

The mean value of these individual proportional differences in weight demonstrates the dry state of the dispersal units, and thus the degree of ripeness.

Results

When the measurements started, the basic take-off force for the dispersal units of *Carpinus betulus* was very great (see Fig. 2 A). One month later, these basic forces had significantly diminished, with a mean value equal to approximately half that measured at the outset in September (1.64 N in September reducing to 0.68 N ± 0.21 N on October 15). However, by November 4, these basic forces had significantly decreased yet again, reaching an average value of
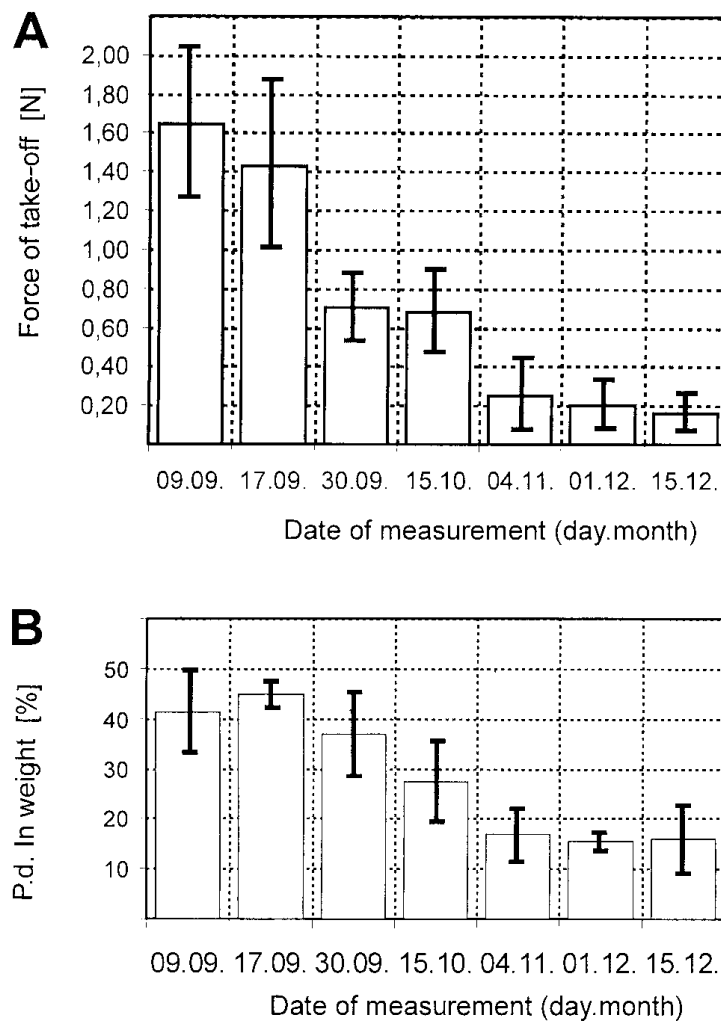
Fig. 2. Bar chart to representing (A) the basic forces in take-off (in N), and (B) the proportional differences in weight (in %) of *Carpinus betulus*.

0.25 N ± 0.18 N. At that point, the basic force for diaspore take-off was eight times smaller than at the beginning in September (in fact, dispersal units were then separated from the mother plant by strong winds, with the result that by January no more measurements were possible).

This decreasing trend also became transparent in terms of proportional weight differences (see Fig. 2 B). It is interesting to note that the level of the basic forces was reflected very accurately by smaller differences in weight. From November, the proportional difference in weight remained at a low level (16.7 ± 5.2 % on November 4, 15.4 ± 1.8 % on December 1, and 15.9 % ± 6.7 N on December 15), and was significantly lower than before. Dried dispersal units of *Carpinus betulus* weigh approximately 0.05 g.

Furthermore, the initial level of basic force on September 30 (see Fig. 2 A) was also reflected by differences in weight, although there was clearly a time delay (see Fig. 2 B, 36.9 ± 8.2 % on September 30, compared to 44.8 ± 2.5 % on September 17). However, a significant graduation was measured in the mid-October (27.4 ± 8.1 % on October 15, compared to 44.8 ± 2.5 % on September 17).

Measurement of basic forces of *Clematis vitalba* showed a wide variation, primarily because the dispersal units were arranged in umbel-like aggregates (HEGI 1981). Furthermore, the dispersal units were very small, which made attaching them with the crocodile clip very difficult. Finally the dispersal units came off immediately if laterally bent. However, if pulling straight, as shown in Fig. 1 was possible, the basic take-off force was measured via the spring scale. Variation was extremely great, a minimum of 0.01 N and maximum of 0.6 N resulting. In *Clematis vitalba*, the mean basic force value for diaspore take-off was 0.18 ± 0.15 N.

Time tunnel experiments with *Clematis vitalba* revealed some very interesting effects (see Tab. 1). Increasing wind velocity from 1 m/sec to 10 m/sec with laminar flow caused the entire dispersal unit aggregate to turn into the wind. No dispersal unit was able to separate completely from the aggregate. In a few cases, dispersal units came off at their predetermined breaking point yet remained within the unit aggregate. Increasing wind velocity to 17 m/s resulted in take-off of 2–5 dispersal units on each branch.

In turbulent wind flow 5–8 dispersal units separated completely at a wind velocity of 10 m/s (Beaufort Scale 5). At a wind velocity of 17 m/sec, all 25 dispersal units had been separated within a time-span of 10 sec (see Table 1). The oscillation movements were particularly interesting to observe. After turning into the turbulent wind of 10 m/s, the wind began to sway the branches. At a velocity of 17 m/s, swaying gave way to an oscillation movement, with the dispersal units seemingly shaken off the branch.

Tab. 1. Results of the wind tunnel experiments for *Clematis vitalba*.

Wind flow	Wind velocity [m/sec]	Number of take-offs of dispersal units	Response in wind flow
laminar	1	0	No movement
	10	0	Turning into the wind
	17	2–5	Turning into the wind
turbulent	1	0	No movement
	10	5–8	Turning into the wind, oscillation movement
	17	25	Turning into the wind, strong oscillation movement

Discussion

Investigations of dispersal biology normally focus on two factors: the structure of the 'seeds' (dispersal unit) and their specialized mode of dispersal (LUFTENSTEINER 1982, MÜLLER-SCHNEIDER 1983, BONN & POSCHLOD 1998). In this context, JENNY (1994) coined the very relevant term 'form and function' (also compare PÜTZ & SCHMIDT 1999 'plant construction').

The beginning of dispersal is the transition from a sessile to a mobile phase (KOHLERMANN 1950, BONN & POSCHLOD 1998), an active moment, the most suitable term for which is 'take-off'. Surprising is that most experimental investigations of anemochorous dispersal ignore this very important moment. It is assumed, of course, that take-off is an important factor, and that take-off occurs at a number of different wind velocities (MÜLLER-SCHNEIDER 1983). However, detailed information is lacking.

The results of the preliminary investigations we present here provide quantitative data for the first time. The degree of force or wind velocity required for *Carpinus betulus* and *Clematis vitalba* respectively are demonstrated in practice.

The method of force measurement substitutes spring scale force for wind force. All other biophysical patterns have been standardized, i.e. bending and shearing force obtaining at the predetermined breaking point. That this was necessary is demonstrated by the dispersal units of *C. vitalba*. At the same time, artificiality lies in the fact that our method simulates only one wind direction, and that the pulling force acts oppositely to separation resistance (F_{tissue}). In natural circumstances, the wind changes velocity and direction continuously (HÄKEL 1985). In most cases, anemochorus dispersal units are suspended, and natural wind thus impacts them laterally (MÜLLER-SCHNEIDER 1983). However, both test species showed an adaptation: turning their aggregates of dispersal units into the wind. Furthermore, to discover any changes in take-off response, we observed dispersal unit response under turbulent wind flow in the parallel wind tunnel experiments.

Since *Carpinus betulus* has relatively heavy dispersal units (0.05 g, see LUFTENSTEINER 1982), AUGSPURGER & FRANSON (1987) assume that dispersal units of this species are very strongly attached to the mother plant. However, our measurements of the forces necessary for take-off appear to refute this assumption. Take-off force required and differences in proportional weight both decrease as development progresses. We assume that a constant proportional difference in weight is an indication of diaspore ripeness. Thus, in *Carpinus betulus*, the level of take-off force required corresponds to diaspore ripeness. Dispersal units of *C. betulus* ripen in November, subsequently taking off at relative low forces (0.2 N). At the same time, *Clematis vitalba* has small and light dispersal units (0.0014 g, SALISBURY 1942) yet require approximately similar forces to *C. betulus* for take-off (0.18 N).

At this point, the question arises as to whether an estimation of the correlation

between our measured forces and wind velocity is possible. Wind tunnels allow defined conditions, and in this way previous experiments were able to reveal many important facts about dispersal (e.g., LUFTENSTEINER 1982, KADEREIT & LEINS 1988, FELDMAN & LEWIS 1990, SCHMIDT 1991, ANDERSEN 1992, 1993, EMIG & LEINS 1994, MÜLLER 1996). Our experiments with *C. vitalba* led to observation of the following interesting points:

1. Some dispersal units came away from their predetermined breaking point, but did not become separated from the mother plant, becoming caught on other diaspores still attached to the mother plant. Together they form a random cluster of dispersal units, termed 'Kumulokarpie' (LOTHSKA 1968). Separation only occurred when all dispersal units of the cluster had come off. Ecologically-oriented experiments are called for to put us in the picture about the function of these 'diaspore clusters'.

2. HÄCKEL (1985) pointed out that wind is always turbulent; we found that turbulent wind flow has a special effect on *Clematis vitalba*: the oscillation movements signify a movement of branches analogous to the fast movement of a pendulum in wind flow. Admittedly, our observation of these oscillations was in 20-cm-long branches. Experimental evidence is needed to confirm whether these movements only occur in relatively short branches. At the same time, our assumption was that oscillation produces bending forces at the predetermined breaking point, with the dispersal units snapping off. This means that oscillation movement results in diaspore shake off! Oscillation movements are familiar from other topics, e.g. tapered plant stems. In this connection, an interesting biomechanical approach was that of SPATZ & SPECK (2002). However, to our knowledge, oscillation movement in connection with anemochorous dispersal has not been mentioned up to now.

3. Our results show (Table 1) that individual dispersal units take off at a wind velocity of 17 m/s lamiar flow (with no oscillation). It can be expected that this laminar flow wind velocity approximates very closely to the force necessary for take-off in *Clematis vitalba* (0.18 ± 0.15 N). In terms of a quantitative approach, it is possible to estimate that a wind velocity of 20 m/s (laminar flow) results in a force requirement for dispersal unit take-off in *C. vitalba* of approximately 0.2 N.

In general, it can be stated that the validity of force necessary for take-off becomes most evident in relation to dispersal distances. A force defined for dispersal unit take-off implies a defined wind velocity! It is thus possible to define a wind velocity at which the dispersal units of *Carpinus betulus* and *Clematis vitalba* are separated: approximately 20 m/s (see [3]). At the same time, wind velocity is one of the most important factors in the quantity of dispersal (MÜLLER 1996). AUGSPURGER & FRANSON (1987) showed that dispersal distance is proportional to wind velocity. SCHMIDT (1918) calculated that dispersal distances increase four-fold when wind velocity doubles, although GEIGER (1961) and EMIG & LEINS (1994) were not able to confirm this ratio.

Take-off at wind velocities of approximately 20 m/s (as necessary in *Clematis*

vitalba and *Carpinus betulus*) means a relatively large dispersal distance (BLATTNER & KADEREIT 1991). However, dispersal distance also depends on the height of exposure and also diaspore weight (LUFTENSTEINER 1982). Diaspore weight in *Clematis vitalba* is very low (0.0014 g), and thus distances of more than 100 m are likely (long-distance dispersal, i.e. exceeding 100 m, according to LUFTENSTEINER 1982). Furthermore, it can be estimated that the relatively heavy dispersal units of *Carpinus betulus* (0.05 g) are unable to cover such long distances of 100 m and more at a wind velocity of approximately 20 m/s.

A great number of parameters are key in dispersal (FISCHER et al. 1996, THIEDE & AUGSPURGER 1996). Different combinations of all these parameters gives rise to individual dispersal clusters, which vary from species to species (seed shadows, HARPER 1977, MACDONALD & SMITH 1987). 'Take-off' is only one aspect of the important moving complex of dispersal, and, as we have shown in this paper, show specific, species-related strategies (e.g. decrease in required forces in *Carpinus betulus*, oscillation in *Clematis vitalba*). However, at present these 'take-off strategies' are not encompassed by dispersal clusters. Filling this gap in our knowledge will require further investigation of 'take-off strategies'.

Acknowledgements

Literature

ANDERSEN, M.C. 1992: An analysis of variability in seed settling velocities of several wind-dispersed Asteraceae. — Amer. J. Bot. **79**: 1087–1091.
— 1993: Diaspore morphology and seed dispersal in several wind-dispersed Asteraceae. — Amer. J. Bot. **80**: 487–492.
AUGSPURGER, C.K. & FRANSON, S.E. 1987: Wind dispersal of artificial fruits varying in mass, area, and morphology. — Ecology **68**: 27–42.
BLATTNER, F. & KADEREIT, J.W. 1991: Patterns of seed dispersal in two species of *Papaver* L. under near-natural conditions. — Flora **185**: 55–64.
BONN, S. & POSCHLOD, P. 1998: Ausbreitungsbiologie der Pflanzen Mitteleuropas, Grundlagen und kulturhistorische Aspekte. — Wiesbaden: Quelle & Meyer.
BRONSTEIN, I.N. & SEMEDJAJEW, K.A. 1991: Taschenbuch der Mathematik. — GROSCHE, G. ZIEGLER, V. & ZIEGLER, D. (eds). — Stuttgart, Leipzig: Teubner.
CHRISTIANSEN, 2. 1954: Verbreitung — Ausbreitung. — Ber. Dtsch. Bot. Ges. **67**: 344–345.
EMIG, W. & LEINS, P. 1994: Ausbreitungsbiologische Untersuchungen in der Gattung *Campanula* L. — I. Vergleichende Windkanalexperimente zur Samenportionierung bei *C. trachelium* L., *C. sibirica* L. und *C. glomerata* L. — Bot. Jahrb. Syst. **116**: 243–257.
FELDMAN, S.R. & LEWIS, J.P. 1990: Output and dispersal of propagules of *Carduus acanthoides*. — Weed Res. **30**: 161–169.
FISCHER, S.F., POSCHLOD, P. & BEINLICH, B. 1996: Experimental studies on the dispersal of plants and animals on sheep in calcareous grasslands. — J. Appl. Ecol. **33**: 1206–1222.

GEIGER, R. 1961: Das Klima der bodennahen Luftschicht. — Braunschweig: Vieweg.

HÄCKEL, H. 1985: Meteorologie. — Stuttgart: Ulmer.

HARPER, J.L. 1977: Population biology of plants. — London: Academic Press.

HECKER, U. 1981: Windverbreitung bei Gehölzen. — Mitt. Deutsch. Dendrol. Ges. 72: 73–92.

HEGI, G. 1981: Illustrierte Flora von Mitteleuropa (Bd. III). — Berlin: Parey.

JENNY, M. 1994: Diasporenausbreitung in Pflanzengemeinschaften. — Beitr. Biol. Pflanzen 68: 81–104.

JOHNSON, W.C. 1988: Estimating the dispersability of *Acer, Fraxinus* and *Tilia* in fragmented landscapes from patterns of seedling establishment. — Landscape Ecology 1: 175–187.

KADEREIT, J.W. & LEINS, P. 1988: A wind tunnel experiment on seed dispersal in *Papaver* L. sects. Argemonidium Spach and Rhoeadium Spach (Papaveraceae). — Flora 181: 189–203.

KOHLERMANN, L. 1950: Untersuchungen über die Windverbreitung der Früchte und Samen mitteleuropäischer Waldbäume. — Forstwiss. Centralbr. 69: 606–624.

LOTHSKA, M., 1968: Karpologie und Karpobiologie der tschechoslowakischen Vertreter der Gattung *Bidens*. — Rozpr. Ceské Adak. Vêd., Ser. Mat.-Natur., Praha 78: 1–85.

LUFTENSTEINER, H.W. 1982: Untersuchungen zur Verbreitungsbiographie von Pflanzengemeinschaften an vier Standorten in Niederösterreich. — Bibl. Bot. 135: 1–68.

MACDONALD, D.W. & SMITH, H. 1990: Dispersal, dispersion and conservation in the agricultural ecosystem. — In: BUNCE, R.G.H. & HOWARD, D.C. (eds.), Species dispersal in agricultural habitats, 18–34. — London: Belhaven Press.

MATLACK, G.R. 1987: Diaspore size, shape, and fall behaviour in wind-dispersed plant species. — Amer. J. Bot. 74: 1150–1160.

MÜLLER, C. 1996: Experimentelle und strukturelle Untersuchungen zum Ausbreitungsverhalten anemochorer Samenpflanzen. — Diplomarbeit Berlin.

MÜLLER-SCHNEIDER, P. 1983: Verbreitungsbiologie (Diasporologie) der Blütenplanzen. — Veröff. Geobot. Inst. ETH, Stiftung Rübel 61.

PÜTZ, N. & SCHMIDT, K.H.A. 1999: 'Underground plant mobility' and 'dispersal of diaspores'. Two exemplary case studies for useful examinations of functional morphology (plant construction). — Syst. Geogr. Pl. 68: 39–50.

SALISBURY, E.J. 1942: The reproductive capacity of plants. Studies in quantitative biology. — London: Bell.

SCHMIDT, K.H.A. 1991: Fruchtbiologische Untersuchungen an Disseminulen der Apiaceen (Umbelliferen). — Dissertation RWTH Aachen.

SCHMIDT, W. 1918: Die Verbreitung von Samen und Blütenstaub durch die Luftbewegung. — Österr. Bot. Z. 67: 313–328.

SHELDON, J. C. & BURROWS, F.M. 1973: The dispersal effectiveness of the achene-pappus units of selected Compositae in steady winds with convection. — New Phytol. 72: 665–675.

SHELDON, J.C. & LAWRENCE, J. T. 1973: Apparatus to measure the rate of fall of wind-dispersed seeds. — New Phytol. 72: 677–680.

SPATZ, H.-C. & SPECK. O. 2002: Oscillation frequencies of tapered plant stems. — Amer. J. Bot. 89: 1–11.

THIEDE, D.A. & AUGSPURGER, C.A. 1996: Intraspecific variation in seed dispersion of *Lepidium campestre* (Brassicaceae). — Amer. J. Bot. 83: 856–866.

Addresses of the authors:

PATRICK FONGER, Oertzweg 40, D-22307 Hamburg.

Prof. Dr. NORBERT PÜTZ, Institute for Nature Conservation and Environmental Education, University of Vechta, Postfach 1553, D-49364 Vechta. E-mail: Norbert.Puetz @uni-vechta.de