Environmental variability and the initiation of dispersal: turbulence strongly increases seed release

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Dispersal is a critical process in ecology. It is an important biological driver of, for example, invasions, metapopulation dynamics, spatial pattern formation and pathogen movement. Much is known about the effect of environmental variability, including turbulence, on dispersal of diaspores. Here, we document experimentally the strong but under-explored influence of turbulence on the initiation of dispersal. Flower heads of two thistle species (*Carduus nutans* and *Carduus acanthoides*) with ripe seeds were exposed to series of laminar and turbulent air flows of increasing velocity in a wind tunnel. Seed release increased with wind speeds for both laminar and turbulent flows for both species. However, far more seeds were released, at significantly lower wind speeds, during turbulent flows. These results strongly suggest a need for more quantitative studies of abscission in the field, as well as dispersal models that incorporate variability in the diaspore release phase.

Keywords: seed abscission; dispersal; turbulence; wind dispersal; wind tunnel

1. INTRODUCTION

Dispersal is an important biological process, fundamental to the distribution of species in the environment. Our understanding of dispersal processes, and our ability—or inability—to predict dispersal, constrains our capacity to adequately understand and predict spatio-temporal patterns (Nathan & Muller-Landau 2000; Levin *et al.* 2003). This is true for fundamental theoretical issues in population and community ecology, biodiversity and biogeography (e.g. Hanski 2001; Hubbell 2001; MacArthur & Wilson 1967), as well as for a number of ecological applications, such as forecasting and management in conservation, harvesting, pest control and epidemiology (Shea *et al.* 1998; Geertsema *et al.* 2002; Clark 2003). Thus, accurate quantitative descriptions of dispersal are crucial.

The quantification of dispersal is a rapidly developing area of research (Levin *et al.* 2003; Nathan *et al.* 2003). For plants, great progress has been made in measurement and modelling of wind dispersal (Greene & Calogeropoulos 2002; Nathan *et al.* 2002; Levin *et al.* 2003). Mechanistic models of wind dispersal have been developed to account for the effects of diaspore morphology, release heights, horizontal wind speeds and convection on diaspore movement and dispersal distances (e.g. Burrows 1973; Greene & Johnson 1989; Okubo & Levin 1989; Andersen 1991). More recent models also include seasonal wind speed variance

(Nathan *et al.* 2001) and high-frequency fluctuations, i.e. turbulence, during seed flight (Nathan *et al.* 2002; Tackenberg 2003; Soons *et al.* 2004). Including variability in wind patterns during seed flight often improves model predictions of dispersal distances (Skarpaas *et al.* 2004; Soons *et al.* 2004).

A component that is still poorly represented in dispersal models, or more often not represented at all, is the initiation of movement: diaspore release or abscission. Predictions of dispersal distances are often made assuming that seeds are released at random with respect to wind speeds. Several authors have noted that this is not the case for natural seed abscission (see e.g. Greene & Johnson 1992; Schippers & Jongejans 2005). Consequently, it has been suggested that mechanistic models should be modified to account for this, for example, by introducing a release threshold: a minimum wind speed required to abscise the seed (or fruit) from the mother plant (Burrows 1986). Such release thresholds may have a large effect on dispersal distances (Schippers & Jongejans 2005).

Previous studies of wind dispersed species have shown that seed release changes with seed ripening and environmental conditions such as air humidity (Whalley *et al.* 1990; Greene & Johnson 1992; Ferraniz 2002). Greene & Johnson (1992) showed that ‘wiggling’ the fruit increased release, which suggests that not only phenology, but variability in wind patterns may affect release thresholds. In this paper we present a wind tunnel experiment to explore, in a quantitative way, the effects of turbulence on seed release. This study shows that wind variability critically alters abscission compared to laminar flow results.

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2. MATERIAL AND METHODS

The abscission experiment was carried out using flower heads of two species of wind dispersed thistles (*Carduus nutans* L. and *Carduus acanthoides* L.). These Eurasian-origin thistles are now widespread invasive species in pastures and grasslands in the USA (Skinner *et al.* 2000; Allen & Shea *in press*). Both species disperse exclusively by seed. The flower heads of *C. nutans* are larger (3–5 cm in diameter) and produce more seeds (often several hundred per head; Desrochers *et al.* 1988) than *C. acanthoides* (flower heads 2–3 cm in diameter; 100–200 seeds per head; Feldman & Lewis 1990). The achenes (3–4 mm long; hereafter referred to as ‘seeds’) and the attached plumeless pappi (i.e. pappi consisting of single hairs in contrast to the feather-like structures of *Cirsium* sp.) are similar in the two species, but slightly larger in *C. nutans* (Skarpaas *et al.*, unpublished data). The seeds of both species are readily dispersed by wind, although a large number of seeds often remain in the heads when the plants die in autumn (Skarpaas, personal observation).

Intact flower heads for the abscission experiment were collected from naturalized thistle populations in central Pennsylvania, USA, at the time of seed ripening (June for *C. nutans* and July for *C. acanthoides*). The heads were individually stored in paper bags at room temperature to maintain the heads in their original condition. The experiment was carried out in late July 2004 in a wind tunnel at the Department of Aerospace Engineering, The Pennsylvania State University. In the wind tunnel, the heads were exposed to laminar and turbulent air flows over a range of wind speeds (0.0–12.0 m s⁻¹), covering the range of wind speeds observed in the natural environments of the thistles in Pennsylvania (Skarpaas & Shea, unpublished long-term measurements with 10 s and 20 min resolution).

The experimental design was a cross-over design in which each head was exposed to both laminar and turbulent treatments. Forty heads were split into two groups of twenty (10 randomly selected heads of each species) receiving the turbulent and laminar treatments in opposite orders (turbulent before laminar or vice versa). The exposure of each head to both treatments is important, because it allows us to test for the effect of turbulence while controlling for the effect of the condition of the head, such as ripening, storage history, previous seed release, etc. Some of the heads lost a few seeds in the bags during storage prior to the experiment, particularly the *C. nutans* heads which were stored for longer. However, the cross-over design explicitly accounts for this and other pre-experiment differences among the heads.

In each trial, a head was attached with tight rubber bands to a surrogate stem (a stiff metal rod) with the head centred at 63 cm above the floor in the middle of the upwind end of the tunnel, and subjected to either laminar or turbulent flow. The laminar flow treatment consisted of simple laminar air flow in the tunnel with no obstacles. Turbulence was created by inserting a frame with nine horizontal 1.5 cm thick threaded rods. The rods were placed 1.5 cm apart across the wind tunnel at the height of the flower head, 30 cm upwind. The turbulence generated by this frame was estimated on the basis of hotwire measurements of wind speeds in a vertical profile across the height of the rods. The turbulence intensity T is defined as

$$T = \sqrt{u'^2/\bar{U}},$$

where $\bar{U}$ is the mean wind speed and u' is the eddy velocity, i.e. the instantaneous deviation from the mean wind speed (Glickman 2000). In both laminar and turbulent treatments the air flow was started at zero and turned up to five consecutive levels (dial settings corresponding to approximately 2.0, 3.0, 6.0, 9.0 and 12.0 m s⁻¹ for laminar flow). Each level was held for 30 s. As individual seed releases from the head were difficult to observe directly, especially at high wind speeds, we also observed the seeds as they hit a black mesh screen approximately 4 m downwind from the release point. For each trial we recorded the wind speed at first seed release and the total number of seeds released.

The data were analysed using cross-over analysis in R (Milliken & Johnson 1992; R Development Core Team 2005). This method is designed for cross-over experiments and allows estimation of the effect of turbulence, while appropriately accounting for the dependence between repeated measurements (two wind treatments: turbulent and laminar) on the same heads. To control for differences between the species we included species as a factor. Finally, to test for potential differences in the effect of turbulence arising from the previous exposure history of the heads in the experiment, we included the interaction between wind treatment and the order of treatments in the statistical analysis.

3. RESULTS

Turbulence intensity was consistent across wind speeds ($T=0.15\pm0.02$) and had a large effect on seed release. Flower heads generally released more seeds at lower wind speeds, during turbulent flow than during laminar flow, regardless of the order of treatments (figure 1). Median release speeds for first release during turbulent flow were 4.1 m s⁻¹ for *C. nutans* and 6.1 m s⁻¹ for *C. acanthoides* regardless of treatment order: consistently lower than for laminar flow (≥ 9.0 m s⁻¹ for *C. nutans* and > 12.0 m s⁻¹ for *C. acanthoides*). Note that the means are not directly comparable because in all treatment combinations there were heads that did not release seeds, and hence we only know that their release wind speeds are > 12.0 m s⁻¹. When turbulence was applied first, few heads released seeds during the subsequent laminar flow, leading to dramatic differences between the two treatments (figures 1a and 2a). The difference was still clear, albeit smaller, when laminar flow was applied first (figures 1b and 2b).

For the total number of seeds released, the cross-over analysis revealed a strong and highly significant effect of turbulence (table 1, figure 2). There were also significant differences between the species. As expected on the basis of its higher seed production, *C. nutans* released more seeds than *C. acanthoides* (table 1, figure 2). The estimated negative effect of the order of wind treatments (table 1) shows that fewer seeds were released during a given treatment (turbulent or laminar) when this was applied last, compared to when it was applied first (figure 2). This effect was only marginally significant, however, and there was no difference for laminar and turbulent flow in this respect (the interaction between wind treatment and order was not significant, table 1).

4. DISCUSSION

The main message from this study is that turbulence increases seed release, both in terms of the proportion of

Figure 1. Cumulative proportion of heads of *Carduus nutans* and *C. acanthoides* releasing seeds at increasing wind speeds. Observations (points) and smoothing quadratic splines (lines) for laminar air flow (circles and solid lines) and turbulent air flow (triangles and dashed lines). Each panel shows the result for the given species receiving (a) the turbulent treatment before the laminar treatment or (b) vice versa.

Figure 2. Mean number of seeds ($\pm$ s.e. indicated by error bars) released per head for *Carduus nutans* and *C. acanthoides* during turbulent (T; grey bars) and laminar (L; white bars) air flow (0.0–12.0 m s⁻¹). Each panel shows the result for the given species receiving (a) the turbulent treatment before the laminar treatment or (b) vice versa. The differences among wind treatments (turbulent/laminar) and species are highly significant ($p < 0.01$); the order of treatments is only marginally significant ($p = 0.08$; cross-over analysis; table 1).

heads releasing seeds at any particular wind speed, and in terms of the total number of seeds released per head. This held true in our experiments regardless of species, head condition, or the order of laminar and turbulent flow treatments.

Turbulence may have contributed to higher seed release in several ways. First, turbulent flows increase the probability of extremes of high (and low) wind velocities. The distribution of the turbulent fluctuations may also be right skewed with an increased probability

Table 1. Cross-over analysis of total seed abscission in turbulent and laminar air flows for *Carduus nutans* and *C. acanthoides*. ('Stratum' indicates the error stratum of the cross-over model (Milliken & Johnson 1992). The 'turbulence' variable indicates the effect of turbulent versus laminar flow, 'order' indicates the effect of the second wind treatment versus the first, 'turbulence : order' indicates the interaction between the turbulence treatment and the order of wind treatments, and 'species' indicates the effect of *C. nutans* versus *C. acanthoides*.)

stratum	variable	estimate	p-value
within	turbulence	3.625	0.002
	order	-1.925	0.080
flower head	turbulence : order	1.850	0.465
	species	3.825	0.004

of encountering the high extremes (this is often the case in natural canopies; Katul *et al.* 1997; Poggi *et al.* 2004a). The potential for waving motion of plants is also generally higher in turbulent flows with a wider energy spectrum (e.g. Poggi *et al.* 2004b) overlapping the natural frequency of the plants. However, in our experiments the potential for waving motion was restricted because the flower heads were attached to a stiff pole. In the absence of waving motion, less kinetic energy is extracted from the air by the drag (the drag coefficient is smaller for turbulent flow than for laminar flow; Poggi *et al.* 2004b), leaving more kinetic energy for loosening seeds. Regardless of the details of the physical mechanism, our experiments demonstrate that turbulence increases seed abscission.

To consider realistic seed abscission is important. Unless the biological process is well understood, we will be unable to predict how plant dispersal patterns may respond to environmental variability, much less how such a response may evolve under various selection pressures, e.g. for long-distance dispersal. Long-distance dispersal is a critical biological process, but notoriously difficult to measure, leading to the conclusion that our best tools for estimating long-distance dispersal are mathematical models (Nathan *et al.* 2003). Considerable progress in predicting wind dispersal patterns has been made using mechanistic models (Greene & Calogeropoulos 2002; Nathan *et al.* 2002; Levin *et al.* 2003; Nathan *et al.* 2003), and including wind variability during seed flight in such models has improved model predictions (Skarpaas *et al.* 2004; Soons *et al.* 2004). This study suggests that including realistic seed abscission may lead to further improvement.

A major implication of our results is that ignoring variability in environmental conditions during the seed release phase may result in erroneous predictions of dispersal patterns. Estimates of release thresholds based on mean-field conditions, i.e. laminar flows in wind tunnels, are likely to be too high. Turbulent flow is the rule rather than the exception in natural plant canopies (Raupach & Thom 1981; Finnigan 2000), and since turbulence increases seed release at lower wind speeds, this may lead to shorter dispersal distances than expected under mean-field conditions. For instance, consider the simple ballistic model of dispersal, which is the basis for

several more complex mechanistic models of wind dispersal (Greene & Johnson 1989; Nathan *et al.* 2001): the ballistic equation is $r = HUF^{-1}$, where r is dispersal distance, H is release height, U is horizontal wind speed and F is seed falling velocity. According to this model, a 60% reduction in the wind speed release threshold, as in our experiment, would lead to a 60% reduction in dispersal distance. Furthermore, plants in dense populations may experience more turbulence (Raupach & Thom 1981; Poggi *et al.* 2004b), and hence release seeds more easily and achieve shorter dispersal distances than isolated plants, which are often used as model systems for dispersal measurement (Greene & Calogeropoulos 2002; Skarpaas *et al.* 2005). Thus, turbulence may potentially counteract the positive effect of release thresholds suggested by Schippers & Jongejans (2005).

On the other hand, detailed modelling studies of seed flight have shown that turbulence may also increase dispersal distances because structured turbulent eddy motions tend to lift seeds to higher elevations with higher horizontal wind speeds (Horn *et al.* 2001; Nathan *et al.* 2002; Soons *et al.* 2004). There is also an interaction between turbulence and wind speed during seed flight as there is a tendency to higher uplifting by autocorrelated eddies in stronger winds and sparser canopies (Nathan *et al.* 2002; Soons *et al.* 2004; Nathan & Katul 2005), and by thermal updrafts that tend to develop only in relatively weak winds (Tackenberg 2003). However, the effect of turbulence on the seed abscission phase was not included in any of these studies.

To assess the net effect of turbulence on dispersal distances, dispersal models must account for the effect of wind speeds and turbulence on seed abscission as well as seed movement. This also requires quantification of natural levels of turbulence and seed abscission in the field. Although the turbulence intensities in our study are not too far from natural conditions (Raupach & Thom 1981), using the consistent median release wind speeds as fixed release thresholds is still a simplification. The levels of turbulence created in the wind tunnel are not representative of all natural environments in which the species occur: turbulence intensity in and above plant canopies vary considerably with canopy density and plant waving (Raupach & Thom 1981; Katul & Albertson 1998; Poggi *et al.* 2004b). Moreover, release thresholds are likely to vary with seed maturation and environmental conditions such as humidity (see e.g. Greene & Johnson 1992; Schippers & Jongejans 2005). Field experiments with careful monitoring of phenology and environmental variability are needed to obtain reliable estimates of abscission in natural habitats. Furthermore, additional research is needed on how the relationship between turbulence and abscission varies with, for instance, seed size and shape, aerodynamic properties, and taxonomy.

In conclusion, the present study strongly supports the contention that mean-field conditions and assumptions may not lead to accurate predictions of abscission. Specifically, our experiment highlights the importance of wind variability for seed release, and demonstrates that not only mean wind speeds but wind variability is important to seed release: turbulence lowers release wind speeds and increases seed release. This suggests

that future empirical studies should avoid assessing release thresholds in laminar air flows; estimates based on natural levels of wind variability are needed. Our results further suggest that more theoretical and empirical work is needed to understand the importance of environmental variability for wind dispersal. In particular, there is a need for measurements of seed abscission in the field, and for incorporation of the effects of environmental variability in the seed release phase in models of dispersal.

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REFERENCES

- Allen, M. R. & Shea, K. In press. Spatial segregation of congeneric invaders in central Pennsylvania, USA. *Biol. Invasions*.
- Andersen, M. 1991 Mechanistic models for the seed shadows of wind-dispersed plants. *Am. Nat.* **137**, 476–497. (doi:10.1086/285178)
- Burrows, F. M. 1973 Calculation of the primary trajectories of plumed seeds in steady winds with variable convection. *New Phytol.* **72**, 647–664.
- Burrows, F. M. 1986 The aerial motion of seeds, fruits, spores and pollen. In *Seed dispersal* (ed. D. R. Murray), pp. 1–47. Sydney: Academic Press.
- Clark, J. S. 2003 Uncertainty in ecological inference and forecasting. *Ecology* **84**, 1349–1350.
- Desrochers, A. M., Bain, J. F. & Warwick, S. I. 1988 The biology of Canadian weeds. 89. *Carduus nutans* L. and *Carduus acanthoides* L. *Can. J. Plant Sci.* **68**, 1053–1068.
- Feldman, S. R. & Lewis, J. P. 1990 Output and dispersal of propagules of *Carduus acanthoides* L. *Weed Res.* **30**, 161–169.
- Ferraniz, C. 2002 Regulation of fruit dehiscence in *Arabidopsis*. *J. Exp. Bot.* **53**, 2031–2038. (doi:10.1093/jxb/erf082)
- Finnigan, J. 2000 Turbulence in plant canopies. *Annu. Rev. Fluid Mech.* **32**, 519–571. (doi:10.1146/annurev.fluid.32.1.519)
- Geertsema, W., Opdam, P. & Knopff, M. J. 2002 Plant strategies and agricultural landscapes: survival in spatially and temporally fragmented habitat. *Landscape Ecol.* **17**, 263–279. (doi:10.1023/A:1020228708956)
- Glickman, T. S. (ed) 2000 *Glossary of meteorology*. Boston, MA: American Meteorological Society.
- Greene, D. F. & Calogeropoulos, C. 2002 Measuring and modelling seed dispersal of terrestrial plants. In *Dispersal ecology* (ed. J. M. Bullock, R. E. Kenward & R. S. Hails), pp. 3–23. Oxford: Blackwell Science.
- Greene, D. F. & Johnson, E. A. 1989 A model for wind dispersal of winged or plumed seeds. *Ecology* **70**, 339–347.
- Greene, D. F. & Johnson, E. A. 1992 Fruit abscission in *Acer saccharum* with reference to seed dispersal. *Can. J. Bot.* **70**, 2277–2283.
- Hanski, I. 2001 Spatially realistic theory of metapopulation ecology. *Naturwissenschaften* **88**, 372–381. (doi:10.1007/s001140100246)
- Horn, H. S., Nathan, R. & Kaplan, S. R. 2001 Long-distance dispersal of tree seeds by wind. *Ecol. Res.* **16**, 877. (doi:10.1046/j.1440-1703.2001.00456.x)
- Hubbell, S. P. 2001 *The unified neutral theory of biodiversity and biogeography*. Princeton, NJ: Princeton University Press.
- Katul, G. G. & Albertson, J. D. 1998 An investigation of higher-order closure models for a forested canopy. *Bound.-Lay. Meteorol.* **89**, 47–74. (doi:10.1023/A:1001509106381)
- Katul, G. G., Hsieh, C.-I., Kuhn, G., Ellsworth, D. & Nie, D. 1997 Turbulent eddy motion at the forest-atmosphere interface. *J. Geophys. Res.* **102**, 13 409–13 421. (doi:10.1029/97JD00777)
- Levin, S. A., Muller-Landau, H. C., Nathan, R. & Chave, J. 2003 The ecology and evolution of seed dispersal: a theoretical perspective. *Annu. Rev. Ecol. Evol. Syst.* **34**, 575–604. (doi:10.1146/annurev.ecolsys.34.011802.132428)
- MacArthur, R. H. & Wilson, E. O. 1967 *The theory of island biogeography*. Princeton, NJ: Princeton University Press.
- Milliken, G. A. & Johnson, D. E. 1992 *Analysis of messy data*. New York: Chapman & Hall.
- Nathan, R. & Katul, G. G. 2005 Foliage shedding in deciduous forests lifts up long-distance seed dispersal by wind. *Proc. Natl Acad. Sci. USA* **102**, 8251–8256. (doi:10.1073/pnas.0503048102)
- Nathan, R. & Muller-Landau, H. C. 2000 Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends Ecol. Evol.* **15**, 278–285. (doi:10.1016/S0169-5347(00)01874-7)
- Nathan, R., Safriel, U. N. & 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., Katul, G. G., Horn, H. S., Thomas, S. M., Oren, R., Avissar, R., Pacala, S. W. & Levin, S. A. 2002 Mechanisms of long-distance dispersal of seeds by wind. *Nature* **418**, 409–413. (doi:10.1038/nature00844)
- Nathan, R., Perry, G., Cronin, J. T., Strand, A. E. & Cain, M. L. 2003 Methods for estimating long-distance dispersal. *Oikos* **103**, 261–273. (doi:10.1034/j.1600-0706.2003.12146.x)
- Okubo, A. & Levin, S. A. 1989 A theoretical framework for data analysis of wind dispersal of seeds and pollen. *Ecology* **70**, 329–338.
- Poggi, D., Katul, G. G. & Albertson, J. D. 2004a Momentum transfer and turbulent kinetic energy budgets within a dense model canopy. *Bound.-Lay. Meteorol.* **111**, 589–614. (doi:10.1023/B:BOUN.0000016502.52590.af)
- Poggi, D., Porporato, A., Ridolfi, L., Albertson, J. D. & Katul, G. G. 2004b The effect of vegetation density on canopy sub-layer turbulence. *Bound.-Lay. Meteorol.* **111**, 565–587. (doi:10.1023/B:BOUN.0000016576.05621.73)
- R Development Core Team 2005 R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
- Raupach, M. R. & Thom, A. S. 1981 Turbulence in and above plant canopies. *Annu. Rev. Fluid Mech.* **13**, 97–129. (doi:10.1146/annurev.fl.13.010181.000525)
- Schippers, P. & Jongejans, E. 2005 Release thresholds strongly determine the range of seed dispersal by wind. *Ecol. Model.* **185**, 93–103. (doi:10.1016/j.ecolmodel.2004.11.018)
- Shea, K. et al. 1998 Management of populations in conservation, harvesting and control. *Trends Ecol. Evol.* **13**, 371–375. (doi:10.1016/S0169-5347(98)01381-0)
- Skarpaas, O., Stabbe, O. E., Rønning, I. & Svenning, T. O. 2004 How far can a hawk's beard fly? Measuring and modeling the dispersal of Crepis

- praemorsa. *J. Ecol.* **92**, 747–757. (doi:10.1111/j.0022-0477.2004.00915.x)
- Skarpaas, O., Shea, K. & Bullock, J. M. 2005 Optimising dispersal study design by Monte Carlo simulation. *J. Appl. Ecol.* **42**, 731–739. (doi:10.1111/j.1365-2664.2005.01056.x)
- Skinner, K., Smith, L. & Rice, P. 2000 Using noxious weed lists to prioritize targets for developing weed management strategies. *Weed Sci.* **48**, 640–644.
- Soons, M. B., Heil, G. W., Nathan, R. & Katul, G. G. 2004 Determinants of long-distance seed dispersal by wind in grasslands. *Ecology* **85**, 3069–3079.
- Tackenberg, O. 2003 Modeling long-distance dispersal of plant diaspores by wind. *Ecol. Monogr.* **73**, 173–189.
- Whalley, R. D. B., Jones, T. A., Nielson, D. C. & Mueller, R. J. 1990 Seed abscission and retention in Indian rice grass. *J. Range Manage.* **43**, 291–294.