Seed release by invasive thistles: the impact of plant and environmental factors

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Dispersal is a key process in biological studies of spatial dynamics, but the initiation of dispersal has often been neglected, despite strong indications that differential timing of dispersal can significantly affect dispersal distances. To investigate which plant and environmental factors determine the release of plumed seeds by the invasive thistles *Carduus acanthoides* and *Carduus nutans*, we exposed 192 flower heads of each species to increasing wind speeds in a full-factorial wind tunnel experiment with four air flow turbulence, three flower head wetness and two flower head temperature levels. The number of seed releases was highest under dry and turbulent conditions and from heads that had already lost a considerable number of seeds, but was not affected by flower head size, head angle or temperature. Inspection of the trials on video showed that higher wind speeds were needed to meet the seed release threshold in laminar flows and for *C. acanthoides* heads that had been wet for a longer time. Species differences were minimal, although seed release was more sensitive to lower levels of turbulence in the larger-headed and more open *C. nutans* heads. Knowledge of seed release biases towards weather conditions favourable for long-distance dispersal improves our understanding of the spread of invaders and allows managers to increase the efficiency of their containment strategies by applying them at crucial times.

Keywords: seed abscission; seed dispersal; seed release threshold; wind turbulence

1. INTRODUCTION

Information on dispersal is pivotal for understanding the spatial dynamics of species (Shigesada & Kawasaki 1997; Bullock *et al.* 2002, 2006). It is increasingly acknowledged that the initiation of dispersal is not only a crucial component of the dispersal process, but also a relatively unstudied one (Burrows 1986; Isard & Gage 2001; Jongejans & Telenius 2001; Skarpaas *et al.* 2006). However, dispersal initiation biases in time have a strong potential to affect dispersal and spread. For example, they may increase dispersal distances compared with random initiation of dispersal (Schippers & Jongejans 2005).

A much studied dispersal system is the dispersal of plumed Asteraceae seeds by wind in grasslands. It is much debated under which weather conditions long-distance dispersal events take place: on warm days with convectional turbulence but relatively low wind speeds (e.g. Tackenberg 2003; Tackenberg *et al.* 2003), or under very windy conditions with high shear-related air flow turbulences (Soons *et al.* 2004; Greene 2005). In order to make predictions about when seed dispersal is likely to occur, the influences of temperature, moisture, wind speed and wind turbulence on seed release need to be separated. Within a particular day, these environmental factors are, however, strongly correlated. For example, temperature potentially affects release not only directly, but also indirectly through

its effect on air flow turbulence. Thus, these factors are hard to separate in the field, and experimental investigations are needed to disentangle them. Skarpaas *et al.* (2006) showed in a wind tunnel experiment with two *Carduus* species (also Asteraceae) that wind turbulence increases seed release. However, they did not study different levels of turbulence, and to our knowledge no experimental study has investigated the effects of multiple environmental and plant factors on seed release at the same time. In addition to external factors, the intrinsic factor of flower head development (e.g. ripening and opening up) may co-determine when seeds are more likely to release (Whalley *et al.* 1990; Greene & Johnson 1992; Ferrández 2002).

Under what weather conditions and at what developmental stage of the flower heads do seeds actually disperse? In this paper we present a wind tunnel study in which we exposed 192 flower heads of each of the same two *Carduus* species to four levels of air flow turbulence, three levels of wetness and two temperature levels in a full-factorial design to test the hypotheses that each factor separately influences seed release and that warm, dry heads in turbulent air flows release most seeds. Flower heads at different developmental stages (but all ready to release seeds) were used to control for the impact of release phenology of flower heads on the number of releasing seeds.

2. MATERIAL AND METHODS

(a) Study species

Carduus acanthoides L. and *Carduus nutans* L. (Asteraceae) are tall thistles of Eurasian origin that have invaded North

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America and other continents. These congeneric species have very similar life histories: their annual, biennial or longer-lived rosettes die after flowering and are not clonal. Large individuals can produce up to 20 000 plumed seeds that are dispersed by the wind (Kok 2001). However, the two species have contrasting flowering and seed release phenologies (Rhoads & Block 2000): the large flower heads (1.5–4.5 cm in diameter) of *C. nutans* set seed from early July to August, whereas the smaller-headed (1.2–1.6 cm in diameter) *C. acanthoides* plants typically release seeds later and over a longer period of time from the end of July until October. *Carduus acanthoides* flower heads are erect, but *C. nutans* peduncles dry up after flowering, causing the heads to bend sideways or downward ('*nutans*' means nodding).

(b) Flower head collection

The flower heads were collected in single naturalized populations in Central Pennsylvania (*C. nutans*, 77°02' W 40°24' N near Duncannon on 20 July 2005; *C. acanthoides*, 77°53' W 40°49' N in State College between 2 and 8 August 2005). Heads were selected at a stage when they had stopped flowering (the purple flowers had already turned brown), but before the initiation of seed release. The heads (together with part of the stem) were individually stored in open paper bags at room temperature. In the morning of the day on which a particular block of wind tunnel trials was done (5.1 ± 2.1 s.d. days after collection), we selected 26 heads that showed signs of release of ripe seeds. Thus, we obtained dispersal-ready heads without confounding unknown seed releases before collection. The 26 heads per block were randomly assigned to the 24 treatment combinations (four air flow turbulence levels $\times$ three flower head wetness levels $\times$ two flower head temperature levels) and two controls that were saved for examination of the total number of seeds per head.

(c) Wind tunnel

The experiment was performed in a closed-circuit wind tunnel of the Pennsylvania State University aerospace engineering department (see also Dauer *et al.* 2006; Skarpaas *et al.* 2006). The test section was 90 cm high, 60 cm wide and 6 m long. In each trial, a flower head was carefully and firmly attached by its stem with tape to a stiff metal rod (1.1 cm in diameter) that served as a surrogate stem. The head was centred at 46 cm above the floor of the upwind end of the tunnel. Dispersing seeds and pappi were caught by a fibreglass mesh screen (1.6 mm) at the downwind end of the wind tunnel. During each 2 min trial, the wind speed in the wind tunnel was consecutively held for 30 s at 3, 6, 9 and 12 m s⁻¹ to mimic increasing wind speeds within the range of naturally occurring wind speeds at plant height in *Carduus* populations (Skarpaas & Shea 2007). At the start of each block, we determined which dial settings of the fan exactly corresponded to the above wind speeds, while taking into account the current air temperature and pressure in the tunnel and also the air flow resistance caused by the mesh screen and different rod settings (see below). The wind speeds in the tunnel were digitally recorded during each trial.

Turbulence was created by inserting (30 cm upwind from the head) a vertical frame across the wind tunnel with up to 21 horizontal, 1.5 cm thick, threaded rods above each other. The rods were placed 1.5 cm apart and the 11th rod was at the height of the flower head. Four levels of turbulence were created by changing the number of rods in the wind tunnel: in the most turbulent treatment all 21 rods were present. In the

second treatment, only the 11 uneven-numbered rods were in place with 4.5 cm gaps between the rods. In the third treatment, seven rods were placed in positions 2, 5, 8, 11, 14, 17 and 20 with 7.5 cm gaps. In the last scenario, all rods were removed. Any air flow turbulence caused by the remaining frame did not affect the flower head; the air flow was laminar in this no-rod treatment. The turbulence intensities ($I = \sigma_U/\bar{U}$, where $\bar{U}$ is the mean wind speed in down-wind direction and σ_U the standard deviation of U ; Stull 1988) at the centre of the flower heads were 0.0033, 0.0360, 0.0431 and 0.0463 for the 0, 7, 11 and 21 rod treatments, respectively. These turbulence levels were measured at the maximum wind speeds that the fan could generate under the four rod settings: 25, 20, 20 and 17 m s⁻¹. In addition to an increase in the turbulence intensity exactly at flower head height, multiple rods also caused high turbulence above and below the flower head. Additional measurements taken with a single rod in position 11 and a wind speed of 8.2 m s⁻¹ showed that turbulence intensity decreased steeply with vertical distance away from the centre of the flower head.

The first temperature treatment involved storing the heads in a hot ($32.8^\circ\text{C} \pm 2.2$ s.d.) room, in contrast to keeping them at room temperature ($24.6^\circ\text{C} \pm 0.64$ s.d.). These temperatures match temperature ranges recorded in Pennsylvania during the release period. The wetness treatments mimicked the effects of dew and rain as follows: one-third of the heads were kept dry and one-third (while still in the paper bag) were sprayed with 0.8 ml water just before the start of the trial in which a head was used (to mimic light rain or dew just before heavy winds). The remaining one-third of the heads were sprayed with the same amount of water at the start of a whole block and the paper bags with those wetted heads were individually put in closed, plastic ziploc bags to ensure that these heads remained wet for a period of 1–3 hours (to mimic release from heads during prolonged humid weather conditions) before testing. The paper bags with dry heads were also closed in ziploc bags for consistency. All bags were stored and moved carefully to avoid unnecessary agitation.

The 24 trials with different treatment combinations within each block were carried out in the following order for logistical reasons: the three wetness treatments were nested in time within the two temperature treatments (first the heads stored at room temperature and second the heads stored at higher temperature), which were nested within the four turbulence treatments. The order of the four rod settings was randomized within each block. The eight blocks with the earlier flowering *C. nutans* were tested between 25 July and 3 August 2005, and the eight *C. acanthoides* blocks between 5 and 11 August 2005, to correspond to the field release periods as closely as feasible.

(d) Measurements

The seeds and pappi that fell from a flower head before its wind tunnel trial were stored separately from the seeds and pappi that were collected after the trial from the mesh screen at the downwind end of the tunnel. The flower head and the seeds and pappi that were not released during the trial were stored in yet another bag. In the laboratory we separated and counted the good (filled and potentially viable) from the bad (small, shrivelled or predated) seeds for the 'before', 'during' and 'after' samples separately for each head. We also counted the number of pappi that released during a trial. The diameter of the bottom of the flower head was measured to determine its size. We counted the egg cases of the main floral herbivore

Table 1. Binomial regression models of whether flower heads dispersed any seeds during their trial or not. (All interaction terms of the levels of the turbulence, wetness and heat treatments, the main effect of heat and the covariates flower head diameter and angle were not significant and were left out of the models. Turbulence did not significantly influence whether or not any *C. nutans* seeds release and was removed from the regression model for that species. ^(*) $p < 0.1$; $*$ $p < 0.05$; $**p < 0.01$; $***p < 0.001$.)

	<i>Carduus acanthoides</i>		<i>Carduus nutans</i>	
	estimate	<i>z</i>	estimate	<i>z</i>
intercept	0.169	0.34	2.322	3.49***
no. of seeds already fallen	0.044	2.24*	0.016	2.01*
(no. of seeds already fallen) ²	−0.001	−2.74**	−0.000	−1.80 ^(*)
wetness: just wet	−0.435	−0.92	−0.530	−0.69
wetness: long wet	−1.069	−2.35*	−1.476	−2.18*
turbulence: 7 rods	2.053	3.73***		
turbulence: 11 rods	1.633	3.27**		
turbulence: 21 rods	1.422	2.96**		

Table 2. Analysis of covariance of the number of seeds released (log transformed after adding 1) in the wind tunnel experiment. (Only heads from which at least one seed released were included in this analysis. The main factors were air flow turbulence, flower head wetness and flower head temperature. The order of the covariates (the number of seeds that had already fallen from the flower head, the square of that number, the diameter of the flower head and its vertical angle) did not influence whether or not they were significant. Random block effects were accounted for in the error term of the model. ^(*) $p < 0.1$; $*$ $p < 0.05$; $**p < 0.01$; $***p < 0.001$.)

	<i>Carduus acanthoides</i>			<i>Carduus nutans</i>		
	d.f.	MS	<i>F</i>	d.f.	MS	<i>F</i>
no. of seeds already fallen	1	0.21	0.48	1	9.03	10.57**
(no. of seeds already fallen) ²	1	2.27	5.09*	1	13.12	15.35***
flower head diameter	1	3.63	8.13**	1	0.26	0.30
flower head angle	1	1.37	3.06 ^(*)	1	0.20	0.23
turbulence	3	2.78	6.23***	3	8.45	9.89***
wetness	2	4.64	10.40***	2	14.75	17.26***
temperature	1	0.70	1.57	1	0.02	0.03
turbulence × wetness	6	0.99	2.21*	6	0.68	0.79
turbulence × temperature	3	1.32	2.95*	3	1.53	1.79
wetness × temperature	2	0.01	0.01	2	0.21	0.24
turbulence × wetness × temperature	6	0.44	0.98	6	0.63	0.73
residuals	107	0.45		137	0.85	

in North America, *Rhinocyllus conicus* Frölich (Harris 1984), between the bracts of the flower head to determine the level of herbivory on the flower head.

All trials were recorded on video tapes, which were later analysed to determine at what time the first pappus released from a flower head and to measure the angle of the flower head in the plane of the wind tunnel on a continuous scale from 0° for upright heads, 90° for heads that pointed exactly downwind and > 90° for downward hanging heads. We also noted how many pappi (if any) were hanging loosely from the flower head at the beginning of the trial.

(e) Data analysis

The effects of the different treatments on seed release from the heads (excluding pappi that hung loosely at the beginning of a trial) were analysed in two steps: we first fitted binomial regression models to investigate which treatments and covariates influenced whether flower heads released any seeds or not; next we performed an analysis of co-variance (ANCOVA) to study how the treatments and covariates influenced the number of releasing seeds from the heads that released at least one seed. This response variable was log transformed (after adding 1) to increase normality. Flower head development was included in these models using the

following covariates: the number of seeds that had already released from the head within the bag before the start of the trial, and the square of the number of these 'before' seeds (to test for quadratic relationships). Flower head diameter and angle were also included as covariates. We initially included these covariates and all interactions between the treatments in the experiment (turbulence, wetness and temperature) in the analyses, but removed non-significant parameters from the final binomial regression models. Because the number of seeds per head differs considerably between the two species, separate analyses were done for each species. The effect of turbulence, wetness and heat on the time to first pappus release (ignoring any pappi that hung loose at the start) was studied with parametric survival regression models with Weibull distributions. All statistical tests were done in R (R Developmental Core Team 2007).

3. RESULTS

In both species, keeping the heads wet for a longer time decreased the chance that any seeds released at all in the wind tunnel experiment (table 1) and also decreased the number of releasing seeds when seed release did occur (table 2). Applying the same amount of water just before

Figure 1. Relationships between the number of seeds released during the wind tunnel experiment and levels of (a,b) air flow turbulence (increasing with the number of rods in the wind tunnel), (c,d) flower head wetness (dry, just wet or long wet), (e,f) flower head storage temperature (room or hot) and (g,h) flower head development stage (as quantified by the number of seeds that had already fallen from a head before a trial). Different letters within a panel signal significant contrasts in analyses of variance of the log-transformed (after adding 1) number of released seeds (see ch. 12 in [Crawley \(2005\)](#) for contrast analyses in R). The bar plots contain back-transformed means and standard errors.

the trials had less effect on seed release ([figure 1](#)), suggesting that the closing and sticking of the pappi is a gradual process that takes time. In laminar air flow, more *C. acanthoides* heads (52%) did not disperse any seeds at all than in the turbulent air flows (19%), but turbulence did not influence the percentage (10%) of *C. nutans* heads without any seed release ([table 1](#)). The variance in the number of seeds released from the flower heads was significantly explained not only by flower head wetness, but also by air flow turbulence and the stage of development of the head ([table 2](#)). In both species, fewer seeds dispersed in laminar than in turbulent air flow ([figure 1](#)). The number of releasing *C. acanthoides* seeds increased continuously with

increasing turbulence levels. However, once releasing seeds, the nodding heads of *C. nutans* were more sensitive to turbulence, as even at the lowest turbulence level three times more seeds released than in the laminar air flow. Storage temperature had no significant effect on seed release ([figure 1](#)) and did not interact with wetness, as initially expected. Small significant interactions did occur in *C. acanthoides* between turbulence levels and both wetness and temperature ([table 2](#)). Flower head development did matter; a quadratic relationship with the number of seeds dropped before the trials added significantly to the explanation of whether seed release occurred at all ([table 1](#)) and of the variation in seed release numbers ([table 2](#)). This

Figure 2. The proportion of flower heads that had not yet released any seeds through time. Survival analyses were applied to test whether the different levels of (a,b) air flow turbulence, (c,d) flower head wetness and (e,f) temperature influence the rate at which flower heads start releasing seeds. The wind speeds were increased every 30 s during the 2 min trials. Different letters within a panel signal significant contrasts.

shows that for flower heads in an early seed release stage, seed release increased with the number of seeds that had previously dispersed (figure 1). When a high proportion of available seeds had dispersed before the trial, however, the number of seed releases during the trial decreased, because fewer seeds remained (the average total number of seeds in the control heads was 98 (with a 53–149 range) for *C. acanthoides* and was 304 (177–626) for *C. nutans*).

Flower head diameter (mean for *C. nutans* $2.99 \text{ cm} \pm 0.037 \text{ s.e.}$ with $n=192$; for *C. acanthoides* $1.38 \pm 0.028 \text{ cm}$, $n=192$) influenced the number of releasing seeds only in *C. acanthoides* (table 2). The diameter did significantly explain total seed number in the control heads of *C. nutans* ($t=2.37$, $p=0.034$ in a generalized linear model with quasi-Poisson error distribution, $n=15$ as one outlier was omitted: a small head with many seeds), but not in the

C. acanthoides control heads ($t=0.71$, $p=0.49$, $n=16$). The flower heads of *C. nutans* (also known as nodding thistle) did indeed point significantly more downwind (mean angle of 66° ranging from 0° to 175° ; $F=125$, $p<2.2 \times 10^{-16}$, $n=384$) than the more upright *C. acanthoides* flower heads (mean angle of 29° ranging from -30° to 135°). These angles, however, did not explain variation in seed releases (table 1). Only a few egg cases of the musk thistle weevil *R. conicus* were encountered: 16 on eight different *C. acanthoides* flower heads and 13 on 10 different *C. nutans* heads (on average 0.077 and 0.063 egg case per head, respectively). Since egg case densities need to be much higher to affect seed production (Sezen 2007), the number of egg cases did not add significantly ($p>0.11$ in both species) to the explanation of the seed release variation, and this covariate was therefore not included in the ANCOVAs.

Examination of the video tapes revealed that, overall, 15% of the heads started releasing pappi at a wind speed of 3 m s^{-1} , 41% at 6 m s^{-1} , 20% at 9 m s^{-1} and 6% at 12 m s^{-1} , whereas 17% of the heads did not release any pappi at all. The first pappus was often released when the wind speed was just increased to the next level, resulting in peaks just after 30 and 60 s in the frequency distribution of the release times of the first pappi from all different heads. *Carduus acanthoides* heads started releasing pappi significantly sooner (i.e. at lower wind speeds) in the three turbulent air flow treatments combined than in laminar air flow ($z = -3.97$, $p < 0.001$; figure 2). This was, to a lesser extent, also true for *C. nutans* (laminar air flow versus the rods with 7.5 cm gaps: $z = -2.78$, $p = 0.0055$), although the decrease in non-releasing heads in the trials with the two highest levels of turbulence was not significantly ($p > 0.06$) lower than that in the no turbulence trials (i.e. seeds ready to disperse were released at low turbulence levels). Stronger wind speeds were also necessary to start pappus release from *C. acanthoides* heads that had been wet for more than half an hour ($z < -2.80$, $p < 0.0051$ compared with the dry and just wet treatments; figure 2). Heads that were wetted just before their trials, however, started to release pappi at the same rate as dry heads ($z = -1.26$, $p = 0.21$). Prior storage temperature had no influence on the starting time of seed release (*C. acanthoides*, $z = 0.78$, $p = 0.44$; *C. nutans*, $z = -0.68$, $p = 0.50$), and did not interact with wetness as had been hypothesized.

4. DISCUSSION

We have shown that seed release in *C. nutans* and *C. acanthoides* is determined by wind speed, turbulence, wetness and flower head development. These findings predict that under field conditions seed dispersal events will be biased towards dry weather conditions with strong and turbulent air flows.

Maternal plant traits that are known to influence seed dispersal are the above-ground height at which seeds are released, and the positioning of seed production within the inflorescence and surrounding vegetation: higher and more protruding flower heads give their seeds better opportunities to escape the vegetation and to disperse on stronger winds (Jongejans & Schippers 1999; Soons *et al.* 2004). Given our finding that the sensitivity of seed release to weather conditions such as humidity and wind turbulence changes with the phenology of the flower head, it is clear that selective forces may also affect the timing of seed dispersal by means of the rate at which seeds in flower heads become ready for release. The two congeneric plant species in our study largely showed the same patterns of seed release, but there were also interesting differences. Seed release in the species with larger flower heads, pappi and seeds, *C. nutans*, was more sensitive to low levels of turbulence, whereas increasing turbulence increasingly enhanced seed release from the smaller-headed *C. acanthoides*. The larger pappi of *C. nutans* seeds were more exposed to the wind since the heads open up more than the heads of *C. acanthoides*. Another potentially important difference between these species is that the flower heads of *C. acanthoides* contain fewer seeds, and those seeds are released over a shorter time interval (we had to repeatedly collect flower heads of

this species in order to have enough flower heads that were ready to release seeds on the different trial days). Thus, individual *C. acanthoides* flower heads seem to sample winds within a relatively short time interval, whereas the *C. nutans* heads probe a longer time period, but are more sensitive to low turbulence levels. Detailed field observations or model simulations will be necessary to investigate what these species differences mean for average and long-distance seed dispersal. Comparison with other species would also be informative.

Wetness of the pappi strongly reduced the number of releasing seeds. This may not surprise anyone who has seen wet Asteraceae flower heads with closed pappi sticking together, but this effect has never been quantified and is likely to be very important for a dispersal bias towards dry weather conditions during which dispersing seeds are not at risk of being driven to the ground by rain. Although wet pappi may occasionally be released at relatively strong wind speeds (figure 2), the dispersal distances are expected to be significantly greater under dry conditions. Humidity also plays a role in the abscission of maple (e.g. *Acer saccharinum* L.) samaras: the separation layer between the fruit and the tree dries up and breaks at a higher rate under dry conditions (Greene & Johnson 1992). However, as our study showed, humidity affects the release of plumed Asteraceae seeds in a different way: the humidity effect is mediated through the pappi and appears to be independent of the detachment of the seed from the receptacle. In future studies we plan to investigate the effect of the realistic alternation of drying and wetting by dew or rain on the threshold for the release of plumed seeds.

(a) Consequences of release biases for seed dispersal

Species differences in how and for how long individual flower heads present seeds to the wind need to be considered in the light of daily fluctuations in weather conditions. Although the effects of wind speed, turbulence and wetness only interacted for *C. acanthoides*, these meteorological parameters do often follow predictable daily patterns and are thus correlated in time: surface heating by the Sun in the morning causes air to rise, which will cause horizontal wind in the boundary layer to replenish the risen air (Lowry & Lowry 1989). At the same time, surface heating will both warm and dry up flower heads in the field. In addition, turbulence (which turned out to be a major determinant of seed release) is directly dependent on these meteorological parameters: mechanical turbulence depends on the wind speed and thermal turbulence on surface heating. Both types of turbulence normally peak in the afternoon.

Greene (2005) has shown in a short field study that dandelion seeds disperse at higher than average wind speeds. Indirect support for seed release biases towards higher wind speeds comes from the comparison of *Carduus* dispersal studies in the field (O. Skarpaas & K. Shea 2003 and 2004, unpublished data): strikingly different dispersal kernels were obtained from a one-month seed trap study around a thistle patch and from a study in which seeds were released and tracked individually. In natural or planted seed sources, seed release occurs naturally and is probably biased towards higher wind speeds. The role of different forms of turbulence will add to the complexity of this story. Different summer days during the dispersal

season may differ strongly in whether either mechanical or thermal turbulence dominates. Since these different types of turbulence relate to different modes of seed dispersal by wind (either strong wind with shear-induced eddies or weak wind but with larger and more autocorrelated eddies; Nathan *et al.* 2002; Tackenberg 2003; Soons *et al.* 2004; Greene 2005), it will be interesting to investigate how these two types of weather conditions are sampled by plants releasing their seeds in the field.

The decreasing seed release threshold with the development of flower heads (as proxied in our study by prior seed release), together with the sampling bias towards dry weather with large air flow turbulence and the positively related co-occurrence of these different environmental cues, will most probably lead to increased dispersal distances compared with a null model in which seeds are released independently at random moments in time or at mean weather conditions. To quantify the magnitude of such increased dispersal distances, mechanistic dispersal models that incorporate measured weather data, flowering phenology and dynamic seed release thresholds may prove vital. For example, Schippers & Jongejans (2005) have shown that median distances potentially increase twofold if seed release dynamics is included, while long-distance dispersal increased by a factor of four to seven, though their model lacked an experimental underpinning of the mechanism of seed release. The seed release biases reported in this paper will indeed have a substantial impact on spread rate estimates, since Skarpaas & Shea (2007) showed with a mechanistic model for these *Carduus* thistles that projected population spread rates are very sensitive to both the wind speed and the level of turbulence at which seeds disperse.

The experiment presented in this paper independently varied several important seed release-related factors for the first time, and answered many unsolved questions. This allows us to identify directions for further investigations needed to improve our knowledge of the dynamics of seed release. These in-depth studies on these two *Carduus* species also allow us to develop a broader understanding of factors affecting wind dispersal of seeds from wind-dispersed plants in general. Such information will be vital for seed dispersal models and control management studies: understanding which weather conditions are likely to promote both seed release and long-distance dispersal will allow managers to combine this mechanistic knowledge with weather forecasts to apply their containment strategies at crucial times.

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