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Abstract
Background: Non-random seed release caused by plant responses to weather conditions is important for seed dispersal. Much is known about the effects of wind speed and turbulence, but our understanding of the effects of water loss on seed release is either qualitative, or indirect and phenomenological.
Aims: To quantify the empirical relationship between water loss and seed release.
Methods: Capitula of the invasive thistles *Carduus acanthoides* and *C. nutans* were collected from the field and treated for either 0, 1, or 2 days in the laboratory at three different vapour pressure deficit levels (3.4, 9.5, and 17.0 hPa) to cause a range of water loss values. Total seed release was quantified before and during wind tunnel trials.
Results: Water loss was the only significant predictor of whether or not capitula released any seeds. The number of seeds released was predicted by water loss, capitulum diameter, and herbivore damage, with the same amount of water loss having less effect on larger capitula.
Conclusions: These results represent an important step towards using weather data to predict seed release for many xerochastic species. Incorporating the effects of water loss on seed release into mechanistic seed dispersal models will greatly improve predictions of when and how far seeds disperse.

Key words
Carduus acanthoides; *Carduus nutans*; evapotranspiration; seed dispersal; xerochasty

Introduction
Seed release initiates the seed dispersal process in plants, and has implications for spatial dynamics, genetic structure, population ecology, responses to climate change, and the management of both rare and invasive species (Cain et al. 2000; Nathan and Muller-Landau 2000; Levin et al. 2003; Trakhtenbrot et al. 2005; Jongejans et al. 2008). Therefore, calls have been made for more research on this important topic (Schippers and Jongejans 2005; Kuparinen 2006; Nathan 2006). As more and more researchers investigate the mechanisms underlying seed release, it is becoming increasingly clear that seed release is not a random process, but occurs under certain predictable conditions (Greene and Johnson 1992; Tackenberg et al. 2003; Greene 2005; Skarpaas et al. 2006; Jongejans et al. 2007; Soons and Bullock 2008; Hamilton-Brown et al. 2009; Marchetto et al. 2010b; Greene and Quesada 2011), which may vary by species (Wright et al. 2008).

While initiation of dispersal in some species is more likely during precipitation events (Pufal and Garnock-Jones 2010), a majority of wind dispersed angiosperms and gymnosperms are xerochastic, meaning that drying enhances seed abscission and release (Greene et al. 2008). For many Asteraceae species, including the invasive thistles *Carduus nutans* L. and *Carduus acanthoides* L. (Figure 1), drying causes cohesion tissues located on the outer side of the involucral bracts to lose turgidity and buckle, causing the bracts to be lowered away from the seeds and thus exposing seeds to the wind (Fahn 1990). Drying may also cause contraction of the receptacle away from seeds (Smith and Kok 1984).

The ubiquity of xerochastic plant species suggests that seed dispersal models could be made more realistic and accurate for a wide range of species if weather data describing potential evaporation could be used to mechanistically predict seed release. Two important pieces of information need to be re-examined to accomplish this goal. First, we must predict water loss from inflorescences using weather data. A number of models already exist that use weather data to predict water loss from entire plants (de Bruin and Holtslag 1982; Sumner and Jacobs 2005), and even from capitula separately from vegetative structures (Guilioni and Lhomme 2006). The second necessary piece of information, the relationship between water loss and seed release, must still be documented and is the focus of this paper.

Currently, our understanding of the effects of water loss and weather on seed release is either qualitative or phenomenological. Physiologically, we understand what effects dry conditions have on capitula (Smith and Kok 1984; Fahn 1990) and seed attachment structures (Greene and Johnson 1992). Regression models have also been created to relate weather variables to seed release that include temperature (Wright et al. 2008) or relative humidity (Greene et al. 2008). However, temperature or relative humidity alone is a poor indicator of water loss by plants or of evaporation in general (Anderson 1936; de Bruin and Holtslag 1982; Sumner and Jacobs 2005). Therefore, empirical relationships between water loss and seed release are needed to improve mechanistic models of seed release.

To reach goal of quantifying the relationship between water loss and seed release, field-collected capitula of *C. nutans* and *C. acanthoides* were either evaluated immediately or dried in one of three laboratory drying treatments for 1 or 2 days in order to create a wide range of water loss values before evaluation in the wind tunnel. We expected that greater water loss would lead to increased total seed release both before and during wind tunnel trials.

Materials and Methods
Study species

Carduus nutans and *C. acanthoides* are two thistle species of Eurasian origin that commonly invade roadsides, pastures, and abandoned fields (Desrochers et al. 1988). Both species are major economic pests in North America, New Zealand, and Australia. *C. nutans* and *C. acanthoides* are monocarpic perennials that reproduce exclusively by seed. In Pennsylvania, flowering occurs between May and August for *C. nutans*, and between June and October for *C. acanthoides* (Rhoads and Block 2000). C. *acanthoides* produces many small capitula (15.0 mm ± SE 0.14 in this study), while *C. nutans* produces fewer, larger capitula (26.0 mm ± SE 0.48 in this study). Capitula of *C. acanthoides* produce approximately 56-83 seeds (Desrochers et al. 1988). *C. nutans* capitula can produce 165-256 seeds (Desrochers et al. 1988) or ca. 400 seeds (Sezen 2007). Each dispersal unit consists of an achene attached to a pappus consisting of a ring of filaments; for simplicity, we will refer to dispersal units as seeds. In many species seed abscission from maternal tissues caused by the development of the separation zone and drying of the vascular bundle leads directly to seed release (Greene et al. 2008), but friction caused by surrounding capitulum tissue and between pappus filaments can delay seed release in *C. nutans* and *C. acanthoides* so that seed abscission and release are not synchronous.

Capitulum collection and treatment

Capitula ready to disperse or just starting to disperse seeds were collected from four naturalised populations in Pennsylvania during the summers of 2006 and 2007 (one population per species per year) and placed in individual plastic containers at the time of collection to preserve field moisture levels. *C. acanthoides* populations were located in State College, PA, for both years of the study. *C. nutans* populations were located in Duncannon, PA in 2006 and Carlisle, PA in 2007. Forty-five capitula per species were collected on each of several collection dates to control for potential effects of weather conditions prior to collection. *C. acanthoides* capitula were collected on seven dates from 29 July to 6 August in 2006 and five dates from 26 July to 5 August in 2007. *C. nutans* capitula were collected on three dates from 26 July to 5 August in 2006 and five dates from 15-30 July in 2007. Therefore, a total of 540 capitula of *C. acanthoides* and 360 capitula of *C. nutans* were used in this study.

Temperature and dew point data prior to capitulum collection were collected from the National Climatic Data Center for the closest available weather station locations, State College and Harrisburg, Pennsylvania, USA, to determine prior vapour pressure deficit experiences of capitula in the field. Vapour pressure deficit (VPD) gives the difference between the saturation vapour pressure and ambient vapour pressure and is proportional to evaporation rate (Lowry and Lowry 1989). Therefore, it provides a better estimation of drying conditions than either temperature or relative humidity alone (Anderson 1936). Intuitively, high temperatures coupled with high relative humidity, or low temperatures coupled with low relative humidity, lead to different evaporative conditions than might be expected based on temperature or relative humidity alone, because the air is saturated in one case or cannot hold much water in the other. Radar generated precipitation data from the National Weather Service's Advanced Hydrologic Prediction Service were used to obtain high spatial resolution precipitation data, which was necessary since summer thunderstorms can be only a few km in diameter (e.g. Petterssen 1969).

After collection, the 45 capitula per species were randomly assigned to laboratory drying treatments. There were 15 replicates for the no drying treatment and 5 replicates for each combination of temperature and drying duration. Capitula were either tested immediately in the

wind tunnel, or allowed to dry under one of three different drying treatments for either 1 or 2 days at temperatures and VPDs of cold at a constant 10 °C and 3.4 hPa (± SE 0.25), room temperature at 23 °C (± SE 0.16) and 9.5 hPa (± SE 0.84), and warm at 28 °C (± SE 0.19) and 17.0 hPa (± SE 1.15) respectively. VPD was measured in the laboratory with a sling psychrometer. The plastic container lids were left half open during drying treatments to allow mixing of air, but to prevent seed escape. Capitula were weighed before and after treatments were administered to determine how much water evaporated during drying. This water loss value combines changes in the water content of all capitulum structures, including pappi. In order to disturb each capitulum as little as possible, capitula were weighed inside their containers. These masses included all plant tissues that might have become disassociated from the capitula during drying, such as released seeds.

As a comparison to laboratory treatments, mean VPD in the field in the 24 hours before capitula collection for *C. acanthoides* was 9.4 hPa (± SE 3.6, range 3.8-14.7 hPa), and 11.5 hPa (± SE 1.4, range 8.4-12.6 hPa) for *C. nutans*. Mean field temperatures in the 24 hours prior to collection were 23 °C (s.e. 2.9, range 17.6-27.8 °C) for *C. acanthoides* and 25 °C (± SE 2.7, range 20.2-28.4 °C) for *C. nutans*. Field means average over daily fluctuations in VPD and temperature, whereas laboratory drying treatments were relatively constant. The mean sums of precipitation in the 48 hours before collection were 3.3 mm (± SE 4.6, range 0-13 mm) for *C. acanthoides* and 6.9 mm (± SE 16.7, range 0-39 mm) for *C. nutans*.

Wind tunnel trials

Seed release trials were conducted in a closed-circuit wind tunnel of the Pennsylvania State University's Aerospace Engineering Department with a 0.9 m high, 0.6 m wide and 6 m long test section (see also Dauer et al. 2006; Skarpaas et al. 2006; Jongejans et al. 2007; Marchetto et al. 2010b). Turbulence was created by the insertion of a threaded rod of 1.5 cm diameter held by a wooden frame at capitulum height 30 cm from capitula, because both species have been shown to release more seeds under turbulent conditions than in laminar air flow and because truly laminar flow is rare in nature (Skarpaas et al. 2006; Jongejans et al. 2007). The turbulence intensity, which is equal to the standard deviation of the downstream wind speed divided by the mean downstream wind speed, was less than 0.036 (Jongejans et al. 2007). These wind conditions were chosen so that if a capitulum did not release seeds in the wind tunnel, it would be very unlikely to release seeds in the field under the same physiological conditions. The wind tunnel was calibrated every day to adjust for changes in air temperature and pressure that would affect generated wind speeds.

During each wind tunnel trial, capitula were attached to a 1.1 cm diameter, 46 cm high metal rod. Any seeds and pappi that released before the wind tunnel trial commenced were counted. Wind tunnel trials were conducted at a wind speed of 6 m s^{-1} for 1 minute. A fibreglass mesh screen (1.6 mm) was used to catch any seeds released. These were removed after every trial and counted.

Capitulum dissections

After each trial, capitula were stored and dissected in the laboratory. Capitulum diameter was measured as a proxy for the number of seeds produced by each capitulum (Sezen 2007). In addition, egg cases and pupation chambers (cysts) of the weevil *Rhinocyllus conicus* Froel. (a biocontrol agent) were counted to quantify florivory in each capitulum. This damage is known to reduce seed production (Gassmann and Louda 2001; Sezen 2007).

Statistical Analysis

Four potential covariates were expected to have an effect on response variables (water loss or seed release) in addition to the laboratory drying treatments. First, capitulum diameter information is necessary to correct for differences in drying time and seed production (larger capitula produce more seeds). Second, florivory by *R. conicus* reduces the number of seeds available for release during wind tunnel trials (Gassmann and Louda 2001; Sezen 2007). Finally, both field VPD and precipitation information allow the effect of natural conditions in the field to be quantified. The average VPD in the 24 hours immediately before collection and the sum of precipitation over 48 hours immediately prior to collection were used to provide information about drying conditions in the field. These time periods were chosen because they provided good explanatory power for both species.

To determine the effectiveness of the treatments to induce drying, generalised linear mixed models (LMERs) with quasi-poisson error distributions were used to explain variation in weight (water) loss using R (Crawley 2007; R Development Core Team 2010). Quas-ipoisson generalised linear models use a log link function, meaning that the response variable is log-transformed (Crawley 2007). Room and warm laboratory treatments were compared to the cold temperature treatment. Capitula that were tested in the wind tunnel immediately, without drying treatments, were excluded from the analysis because they experienced no water loss. The interaction between drying treatment and duration was included in the analysis, as well as capitulum diameter and number of *R. conicus* cysts. Collection day was used as a random effect in the analysis. Field VPD and precipitation were also included in the models as covariates to understand the relationship between prior environmental conditions in the field and water loss during drying treatments. Records with missing data, comprising 1.3% and 1.2% of data sets for *C. acanthoides* and *C. nutans*, respectively, were removed from the data sets to enable LMER analyses. Missing values were primarily caused by an inability to determine capitulum diameter and number of cysts for some samples, due to mould that infested some capitula between wind tunnel trials and dissection. Non-significant terms were removed from LMER models using deletion tests based on Akaike information criterion (AIC) values to determine the minimum adequate model (Crawley 2007). Models with a significantly lower AIC value fit the data better (Crawley 2007).

The seed release data were zero inflated, meaning that many capitula did not release seeds either before or during wind tunnel trials. To account for this statistical challenge, the seed release analysis was broken into two parts (Zuur et al. 2009). In the first analysis we used LMERs with binomial error distributions and collection day as a random effect to determine whether water loss, capitulum diameter, or *R. conicus* cysts had a significant effect on whether any seeds were released from capitula (either before or during wind tunnel trials). Interactions between head diameter and water loss as well as head diameter and cysts were included in both parts of the analysis. The second analysis was designed to study how many seeds released. This analysis used the subset of the data where at least one seed was released before or during wind tunnel trials. LMERs with quasi-poisson error distributions and collection day as a random effect were used to determine whether water loss, capitulum diameter, or *R. conicus* cysts had a relationship with the number of seeds that were released, in addition to the interactions listed above.

Results

Capitulum morphology changed with different laboratory drying treatments as water was lost (Figure 1). Cold (10 °C, 3.4 hPa VPD), room temperature (23 °C, 9.5 hPa VPD) and warm (28 °C, 17.0 hPa VPD) laboratory drying treatments caused increasing water loss from both *C. acanthoides* and *C. nutans* capitula (Figure 2). Room temperature and warm drying treatments caused significantly more water loss than the cold treatment (*C. acanthoides* room temperature estimate= 0.66, ± SE 0.04, *P*= 0.014; warm estimate= 0.92 ± SE 0.04, *P*= 2.43*10^{-4}; *C. nutans* room temperature estimate= 0.97 ± SE 0.05, *P*=0.0033; warm estimate= 1.49 ± SE 0.05, P= 3.33*10^{-7}; Table 1). Drying treatment duration was not significantly related to how much water was lost from capitula of either species (although drying duration was marginally significant for *C. nutans*; *P*=0.053). Field precipitation did not have a significant effect on water loss (but was marginally significant for *C. acanthoides*; *P*=0.054). Capitulum collection day explained 0.0% of the total variance in water loss from capitulum for *C. acanthoides*, and 49.0% of the total variance for *C. nutans*.
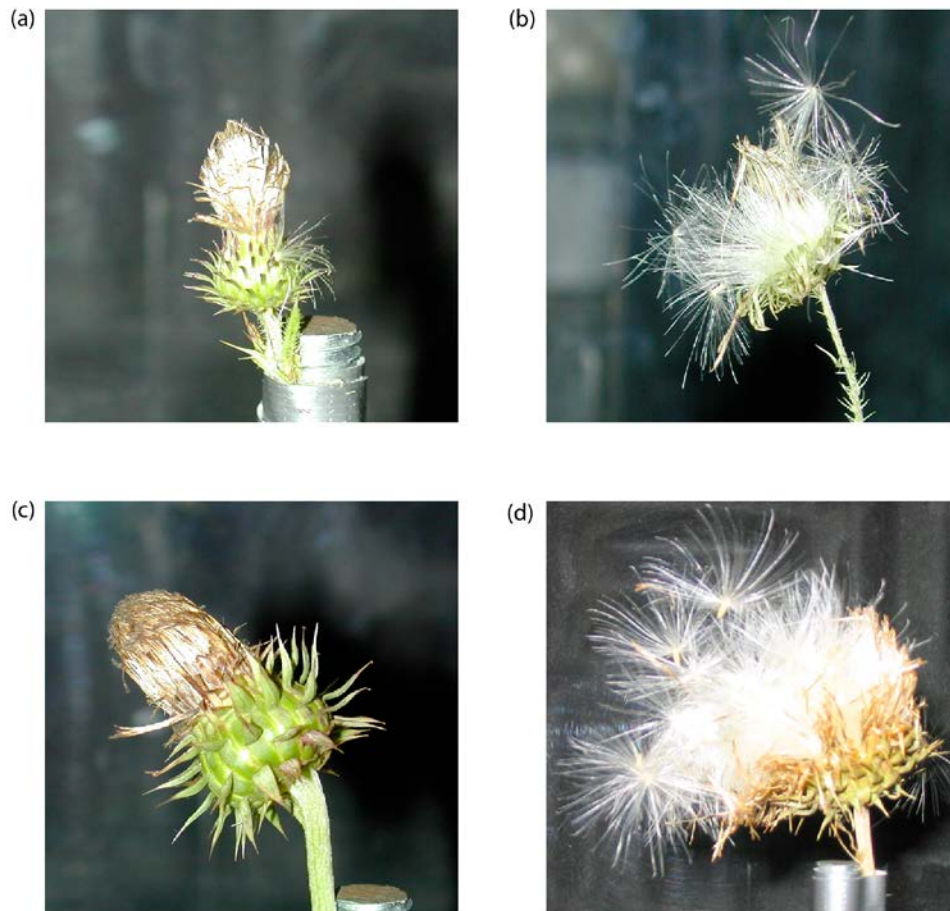

Figure 1 Effects of laboratory drying treatment on capitulum morphology
Panels a and c represent *Carduus acanthoides* and *C. nutans* capitula respectively, dried for 2 days at 10 °C and 3.4 hPa vapour pressure deficit. Panels b and d represent *C. acanthoides* and *C. nutans* capitula respectively, dried for 2 days at 28 °C and 17.0 hPa vapour pressure deficit
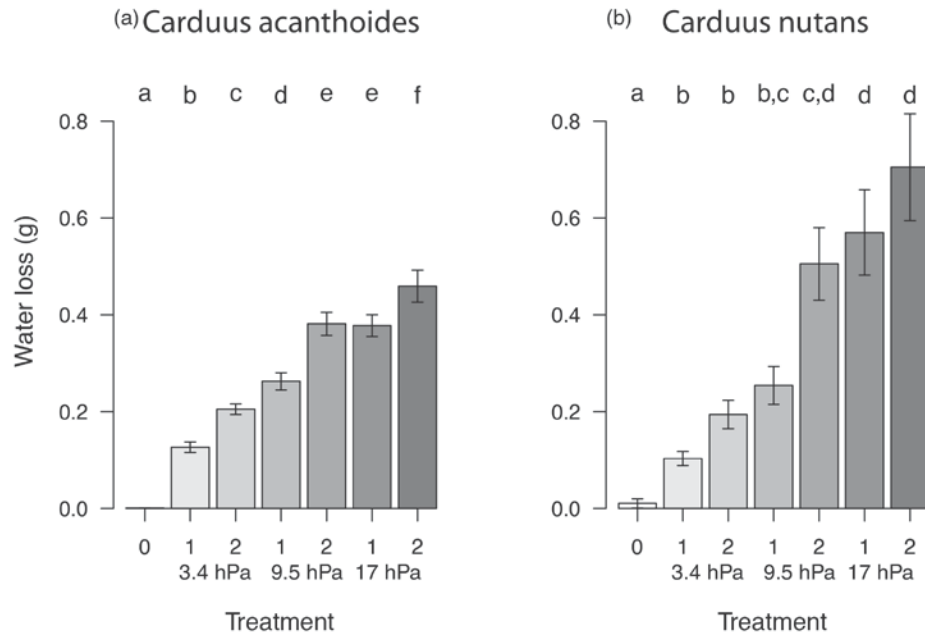
Figure 2 Mean water loss (±SE) from (a) *Carduus acanthoides* or (b) *Carduus nutans* capitula due to drying treatments. Numbers below bars indicate drying durations in days and drying treatment vapour pressure deficits (VPDs). Temperatures for the 3.4 hPa, 9.5 hPa, and 17.0 hPa treatment VPDs were 10 °C, 23°C, and 28 °C respectively. Significance designations come from generalised linear models with quasi-poisson error distributions

    Binomial generalised linear models were used to determine whether water loss, capitulum diameter, or florivory by *R. conicus* affected whether capitula released any seeds (before or during wind tunnel trials). Water loss was the only significant predictor of whether capitula released seeds for both *C. acanthoides* and *C. nutans* (*C. acanthoides* estimate= 4.21 ± SE 0.57, $P= 1.42*10^{-13}$; *C. nutans* estimate= 1.38 ± SE 0.33, $P= 3.17*10^{-5}$, Table 2). However, the fit of the model changes substantially for *C. nutans* if capitula that did not receive a drying treatment (designated as 'controls') are included or excluded (Figure 3). At any observed level of water loss, the model predicts a lower chance of *C. nutans* capitula releasing any seeds if capitula that did not receive a drying treatment are included (Figure 3).

    Generalised linear mixed effects models were used to determine whether water loss, capitulum diameter, or *R. conicus* florivory affected the number of seeds released for the subset of capitula that released seeds. Increasing water loss and capitulum diameter had significant positive effects on the number of seeds released (*C. acanthoides* water loss estimate= 5.36 ± SE 4.27, $P< 2.2*10^{-16}$; capitulum diameter estimate= 0.05 ± SE 0.11, $P< 2.2*10^{-16}$; *C. nutans* water loss estimate= 3.21 ± SE 1.36, $P<2.2*10^{-16}$; capitulum diameter estimate= 0.04 ± SE 0.07, $P= 9.3*10^{-8}$; Table 3). There was a negative relationship between *R. conicus* cysts and the number of seeds released (*C. acanthoides* estimate= -0.33 ± SE 0.74, $P< 2.2*10^{-16}$; *C. nutans* estimate= -0.19 ± SE 0.25, $P< 2.2*10^{-16}$; Table 3). There was also a negative interaction between water loss and capitulum diameter (*C. acanthoides* estimate= -0.17 ± SE 0.22, $P< 2.2*10^{-16}$; *C. nutans* estimate= -0.06 ± SE 0.05, $P< 2.2*10^{-16}$; Table 3) such that for a given amount of water loss, larger capitula released fewer seeds (Figure 3). Capitulum collection day explained 35% of the total variance for *C. acanthoides* and 22% of *C. nutans* (Table 3).
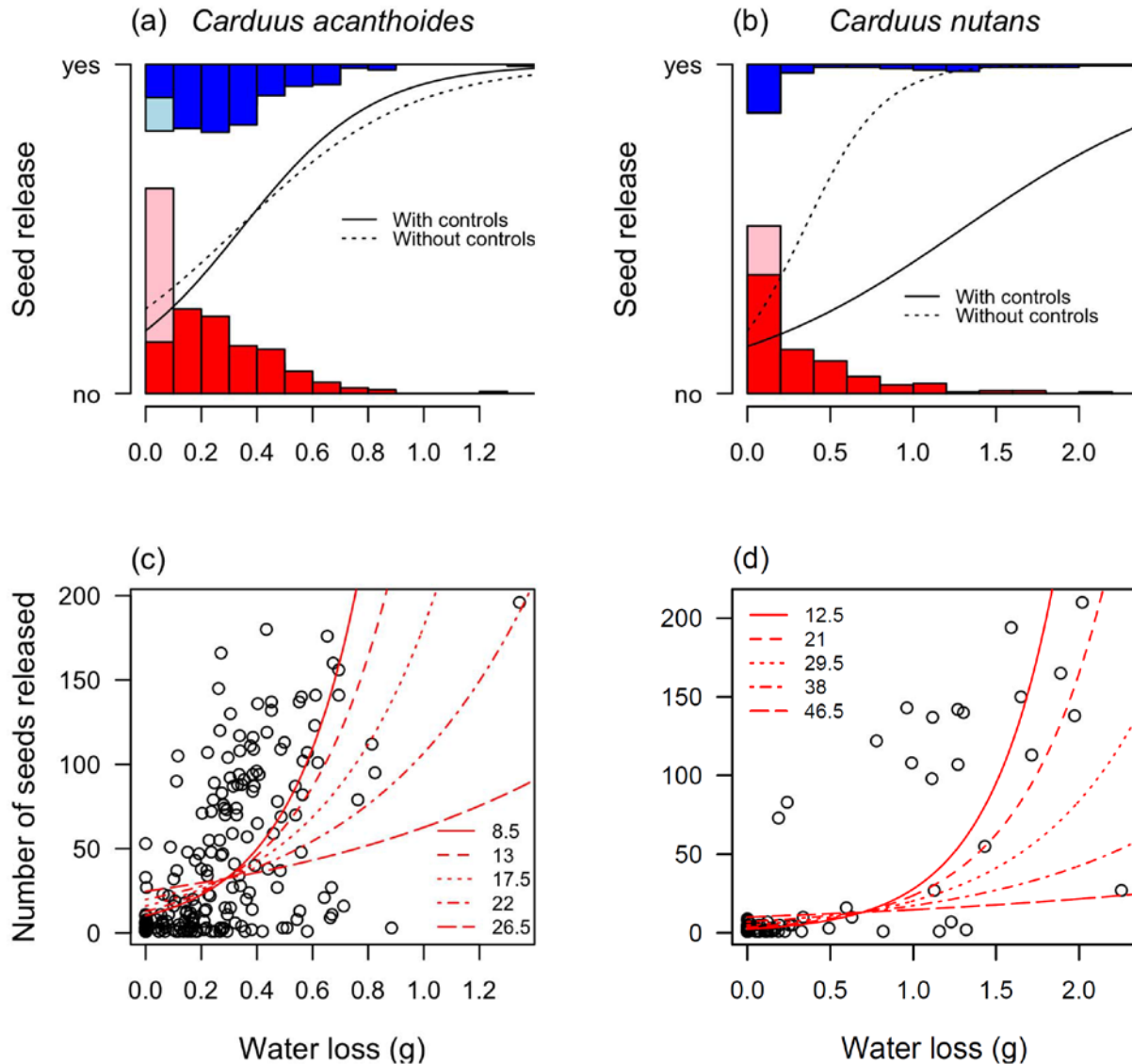
Figure 3 Whether or not *Carduus acanthoides* or *Carduus nutans* capitula released seeds before or during wind tunnel trials (a and b), and if seeds were released how many seeds were released (c and d). Lines represent generalised linear mixed effects models with binomial error distributions and collection day as a random variable fit with and without controls (capitula run in the wind tunnel immediately without drying treatment; a and b) or generalised linear mixed effects models with quasi-poisson error distributions and collection day as a random variable with a range of capitulum diameters (c and d). Light histogram bars in panels a and b show the distributions with capitula that received no drying treatment, while dark bars show the distributions of only capitula which received a drying treatment. The lines in panels c and d represent different model fits for the different capitulum diameters (mm) indicated in the legend. Models in c and d were also fit with the average number of cysts per capitulum for each species, 0.17 for *C. acanthoides* and 2.14 for *C. nutans*.

Discussion

Our results provide an empirical relationship between water loss and seed release: first, whether any seeds release from capitula and second, if release occurs, how many seeds release. The only significant predictor of whether or not seeds release under constant wind conditions is the amount of water lost. Explaining how many seeds are released is more complicated, and requires information on water loss, capitulum diameter, and the level of florivory by the weevil *Rhinocyllus conicus*. There is also a significant negative interaction between water loss and capitulum diameter, so that for the same amount of water lost larger capitula release fewer seeds. This arises because the same mass of water represents a smaller proportion of the total water content of larger capitula. Collection day was an important random variable in most analyses, which may have influenced water loss and seed release through environmental conditions or phenology.

Empirical models describing seed release as a function of water loss are an important part of our ability to mechanistically predict seed release using weather data. A large body of literature already exists that can be used to predict stomatal conductance and evaporation from weather data such as net radiation, air temperature, vapour pressure deficit, and wind speed on a field level (e.g. de Bruin and Holtslag 1982; Sumner and Jacobs 2005) or subdivided into capitula and vegetative structures (Guilioni and Lhomme 2006). The final step in this process would be to verify the assumption that water supply to capitula is greatly reduced during the seed maturation and natural capitulum drying process (Smith and Kok 1984; Fahn 1990). If water supply to capitula is negligible during this period of active drying, then all of the components are available to incorporate with our results and weather data to mechanistically model the effects of evaporative conditions on seed release in the field - with the caveat that in order to know how many seeds release some biological data may be required. The addition of this information to our current knowledge of the effects of wind speed and turbulence on seed release (Greene 2005; Skarpaas et al. 2006; Jongejans et al. 2007; Wright et al. 2008) will greatly improve the predictive power of mechanistic seed release and dispersal models.

Mechanistic seed release models are a key component necessary to understand under which conditions seeds disperse and how far they travel (Jongejans et al. 2007; Soons and Bullock 2008; Wright et al. 2008; Nathan et al. 2011). Seeds that disperse long distances are more likely to have an appreciable impact on migration and gene flow. Long-distance dispersal thus has important ecological and evolutionary impacts, affecting, for example: recruitment, patch colonization and extinction rates, synchrony and stability of population dynamics, meta-community interactions, genetic population structure, and species spread (Nathan and Muller-Landau 2000; Levin et al. 2003; Howe and Miriti 2004; Nathan 2006; Jordano et al. 2007; Abbott 2011). In fact, the timing of seed release may have a greater effect on long-distance dispersal (LDD) than seed terminal velocity, the single most important seed characteristic used in dispersal models (Greene 2005; Schippers and Jongejans 2005; Nathan 2006). Yet, incorporation of mechanistic models describing seed release into dispersal models has lagged behind our understanding of the importance of non-random seed release related to weather variables (Nathan et al. 2011).

The construction of seed release models based on weather parameters as a proxy for water loss will also allow us to begin to use weather projections to understand the impact of climate change on future seed release and dispersal. For instance, temperature and evaporation are expected to increase in the north-eastern United States, where this study was conducted, and instances of heavy precipitation are also on the rise (Hayhoe et al. 2007). Seed release and

dispersal models can be used to evaluate how plant migration may change due to future climate regimes, and to better evaluate the ecological and economic risks of invasive species spread as well as the extinction risk to native species that may not be able to keep pace with niche contraction and expansion (Thomas et al. 2004).

At the same time, it will also be important to examine how changing environmental conditions may interact with plant physiology to influence other dimensions of seed dispersal not addressed by the current study. For example, quicker drying lowers seed release wind speed thresholds in *Daucus carota* by affecting inflorescence morphology (Lacey 1980). This would tend to cause seeds to travel shorter distances under dry conditions, unless compensated for by other mechanisms such as increased frequency of convective updrafts during warm, dry conditions. Alternatively, lower humidity may cause pappi to expand farther, decreasing seed terminal velocity and potentially causing seeds to travel further on average (Sheldon and Burrows 1973).

Our results are broadly applicable to other species because most plants are also xerochastic (Greene and Johnson 1992; Roche 1992; Nathan et al. 1999; Mandak and Pysek 2001; Greene et al. 2008; Wright et al. 2008; Hamilton-Brown et al. 2009). The prevalence of xerochasty suggests that seed release under hot, dry conditions may increase plant fitness, potentially by increasing dispersal distances. For example, in *Pinus halepensis* seed release occurs preferentially during hot, dry conditions (Sharav events), which are associated with increased vertical wind speeds (updrafts) and increased seed dispersal distances (Nathan et al. 1999). Increased occurrences of updrafts associated with warm, dry conditions are also evident in other systems, and have the potential to facilitate long-distance dispersal in some species (Tackenberg et al. 2003). Xerochastic dispersers may also take advantage of increased wind speeds and unstable atmospheric conditions caused by differential surface heating rates in the late morning and afternoon that can increase seed transport (Lowry and Lowry 1989; Greene et al. 2008; Dauer et al. 2009). Large projected population spread rates for *Carduus acanthoides* and *C. nutans* can result when only afternoon wind speeds are used (Marchetto et al. 2010a), when VPD is high and seed release is more likely.

In this paper, we demonstrate a quantitative relationship between water loss and seed release that is an important step towards mechanistic models using weather variables to predict seed release. Incorporating weather variables as a proxy for water loss into models of seed dispersal will improve model performance for xerochastic species. This additional information will be critical, since non-random seed release in the face of the changing climate may have important implications for the spread of invasive plants and range shifts by natives.

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Table 1. Minimum adequate models describing water loss from capitula.
Generalised linear mixed models with collection day as a random effect and quasi-poisson error distributions were used to determine the effects of drying temperature and drying duration treatments, capitulum diameter, florivory by *Rhinocyllus conicus*, as well as the effects of field conditions of temperature and precipitation, on water loss during capitulum drying prior to wind tunnel trials. The interaction between drying treatment and duration was also tested. Models were fitted without controls because they did not receive a drying treatment, and therefore lost no water. The room and warm temperature treatments are compared to the cold temperature treatment. The minimum adequate models based on AIC are shown. Collection date explained 0% of the model variance for *C. acanthoides* and 49.0% for *C. nutans*. The cold, room temperature, and warm treatments represent temperatures of 10 °C, 23 °C, and 28 °C, respectively and vapour pressure deficits of 3.4 hPa, 9.5 hPa, and 17.0 hPa, respectively. The P value for field precipitation for *C. acanthoides* was $P=0.054$. The p value for drying duration for *C. nutans* was $P=0.053$. *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$.

	Carduus acanthoides					*Carduus nutans*				
	Estimate	Std. Error	*t*-value	*P* value		Estimate	Std. Error	*t*-value	*P* value	
Intercept	-1.80	0.03	-53.64 <	2.20E-16	***	-2.32	0.07	-32.23 <	2.20E-16	***
Room temperature	0.66	0.04	16.10	1.35E-02	*	0.97	0.05	18.05	3.30E-03	**
Warm temperature	0.92	0.04	23.33	2.43E-04	***	1.49	0.05	29.17	3.33E-07	***

Table 2. Minimum adequate models describing whether or not capitula released seeds.
Generalised linear mixed models with collection day as a random effect and binomial error distributions were used to determine the effects of water loss, capitulum diameter, florivory by *Rhinocyllus conicus* on whether or not capitula released any seeds before or during wind tunnel trials. Interactions between water loss and head diameter as well as cysts and head diameter were also tested. Controls are included in the analysis presented. The minimum adequate models based on AIC are shown. **, $P<0.01$, ***, $P<0.001$.

	Carduus acanthoides					*Carduus nutans*				
	Estimate	Std. Error	*t*-value	*P* value		Estimate	Std. Error	*t*-value	*P* value	
Intercept	-1.45	0.46	-3.13	0.002	**	-1.79	0.40	-4.46	8.22E-06	***
Water loss (g)	4.21	0.57	7.39	1.42E-13	***	1.38	0.33	4.16	3.17E-05	***

Table 3. Minimum adequate models describing how many seeds released, conditional on any seeds being released. Generalised linear mixed models with collection day as a random effect and quasi-poisson error distributions were used to determine the effects of water loss, capitulum diameter, and florivory by *Rhinocyllus conicus* on the number of seeds released before or during wind tunnel trials, given capitula released any seeds. Interactions between water loss and head diameter as well as cysts and head diameter were also tested. The minimum adequate models based on AIC are shown. Collection date explained 35.0% of the model variance for *C. acanthoides* and 22.0% for *C. nutans*. *, *P<0.5*, ***, *P<0.001*.

	Carduus acanthoides						*Carduus nutans*					
	Estimate	Std. Error	*t*-value		*P* value		Estimate	Std. Error	*t*-value		*P* value	
Intercept	1.98	4.93	0.40		6.15E-07	***	0.75	2.66	0.28		0.030	*
Water loss (g)	5.36	4.27	1.26	<	2.20E-16	***	3.21	1.36	2.36	<	2.20E-16	***
Capitulum diameter	0.05	0.11	0.42	<	2.20E-16	***	0.04	0.07	0.57		9.30E-08	***
Cysts	-0.33	0.74	-0.44	<	2.20E-16	***	-0.19	0.25	-0.75	<	2.20E-16	***
Water loss * capitulum diameter	-0.17	0.22	-0.76	<	2.20E-16	***	-0.06	0.05	-1.28	<	2.20E-16	***