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Shipment and Storage Effects on the Terminal Velocity of Seeds

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Abstract

Mechanistic models of seed dispersal by wind include terminal velocity as the main seed characteristic that influences the dispersal process and hence the resulting dispersal kernels and spread rates. Accurate measurement of the terminal velocity of seeds is therefore pivotal. However, compression during shipment through the post or during storage between collection in the field and terminal velocity measurements in the lab may affect these measurements. To evaluate the effects of shipment and storage on terminal velocity measurements, capitula of *Carduus nutans*, an invasive thistle species from Eurasia, were stored for one to five years and subjected to three different packing treatments. Seeds from capitula were then assessed for terminal velocity values, plume area, seed mass, wing loading, number of filaments per pappus, qualitative assessments of pappus damage, and number of intact dispersal units per capitulum. Compression significantly increased seed terminal velocity. However, storage duration for one to five years did not cause a significant increase or decrease in any of the response variables. The compression treatment was validated by shipment of seeds from New Zealand to the United States. When capitula that will be used for terminal velocity measurements are stored or shipped, they should be packaged in incompressible containers to avoid damage to fragile dispersal structures. Studies using capitula that were originally collected and stored for other purposes, such as transcontinental demographic studies, should rescale observed terminal velocity values to take possible damage into account.

Key words damage; packaging; pappus filaments; seed dispersal by wind; terminal velocity

Introduction

Seed dispersal is an important component of many ecological processes, including the spatial dynamics of populations, population genetics, extinction dynamics, and species responses to climate change (Brown & Kodric-Brown 1977; Ouborg *et al.* 1999; Cain *et al.* 2000; Nathan & Muller-Landau 2000; Levin *et al.* 2003; Skarpaas & Shea 2007). Dispersal also impacts conservation strategies and management plans for limiting invasive species spread (Trakhtenbrot *et al.* 2005; Jongejans *et al.* 2008b). In studies of these ecological processes, there are a host of different models that estimate seed dispersal for different species of wind dispersed plants (Jongejans et al. 2008b). Mechanistic models of seed dispersal by wind can be as complex as stochastic models for the calculation of air particle trajectories (e.g. Nathan *et al.* 2002) or as simple as a basic ballistic approach using release height, horizontal velocity, and vertical velocity (e.g. Greene & Johnson 1989). However, no matter how many parameters are used in a given mechanistic dispersal model, the terminal velocity of seeds (i.e. the speed at which a seed eventually falls in still air after an initial acceleration period: when drag equals gravity) is always included. Therefore, good estimates of terminal velocity for each species that will be modelled are critical.

At the same time, plant demographers are becoming increasingly interested in linking demography with seed dispersal due to recent advances in modelling methodologies (Neubert & Caswell 2000; Wang & Smith 2002; Buckley *et al.* 2005; Jacquemyn *et al.* 2005; Skarpaas & Shea 2007; Jongejans *et al.* 2008a; Soons & Bullock 2008). For researchers with stored seed collections from earlier demographic studies, a tantalizing possibility now exists - to use these sources to quantify rates of spread by measuring seed terminal velocity values. This could be especially interesting for historical seed collections from different time points in the course of an invasion of an exotic species or a range expansion of a native species. For example, the square root of wing loading (which is proportional to terminal velocity) has been found to be positively correlated with time since population founding in *Pinus contorta* ssp. *latifolia* (Cwynar & MacDonald 1987). The ability to use existing collections could also potentially save much time and effort for transcontinental demography studies. It is intuitive that shipment and storage could reduce the usefulness of such collections by degrading the quality of fragile seed dispersal structures, but the extent of this effect is unknown. If the magnitude of the effects of shipment and storage can be quantified, however, not only would the extent of the problem be known, but terminal velocity results could be scaled to offset the influence of these effects on calculated dispersal kernels.

Quantifying the damage caused by shipment or storage on seed dispersal apparati is also important for current biogeographic studies. Many species, including invasives, have large biogeographic ranges over which dispersal characteristics like seed terminal velocity might vary (e.g. Cody & Overton 1996; Jongejans *et al.* 2008a) but see (Nathan *et al.* 1996). The easiest way to determine if seeds from different countries, for example the native and invaded ranges of an invasive species, differ in average terminal velocity would be to collaborate with colleagues on other continents and exchange seeds through the post. This approach would allow greater standardization if all terminal velocities are measured with the same equipment in the same laboratory, while saving travel time and costs. However, it is important to understand the risks associated with this method in order to prevent biased results.

Terminal velocity of plumed seeds, such as Asteraceae species that might be protected within capitula during storage, may be influenced by several factors. Plume area contributes to drag, which decreases terminal velocity values (Sheldon & Burrows 1973; Augspurger 1986; Greene & Johnson 1990; Meyer & Carlson 2001). Seed mass is also important, as heavier seeds are expected to have higher terminal velocities if wing or plume area is constant (Green 1980; Greene & Johnson 1990; Soons & Heil 2002). Both of these terms are incorporated into the definition of wing loading (seed mass divided by plume area), the square root of which was found to be proportional to terminal velocity

(Greene & Johnson 1990; Andersen 1993; Debain *et al.* 2003). Filament length and number can influence wing loading by affecting plume area (Greene & Johnson 1990). Pappus damage caused by shipment or storage, such as gaps in a pappus or bent pappus filaments, could also affect seed terminal velocity. Finally, the number of intact dispersal units (seeds with attached pappi) could affect terminal velocity measurements, because shipment or storage effects that cause a separation of seeds from pappi would reduce the choice of seeds that could be used for these measurements.

To assess the role that storage and transport methods might play in affecting measured values of terminal velocity, we explored these factors for *Carduus nutans* L. (Asteraceae), the nodding or musk thistle. This thistle of Eurasian origin has become a noxious weed in several other continents. Much research focuses on how to control the spread of this species, as well as on the more fundamental question of what has made this species such a successful invader (Shea & Kelly 1998; Shea *et al.* 2005; Jongejans *et al.* 2006; Skarpaas & Shea 2007). Seeds have therefore been stored and shipped across the world for research on the terminal velocities of seeds from different parts of its native and invaded range (Jongejans et al. 2008a). These shipments were well packed to prevent seed escape and inspected by all involved authorities; the impact of such treatments on the terminal velocity of the seeds, however, is unknown.

We hypothesized that packaging methodology and storage duration affect pappus characteristics, such as plume area, maximum filament length, number of filaments, qualitative pappus damage, and the attachment between seeds and pappi, and thus estimates of terminal velocity. We tested this with capitula aged between one and five years old that were stored either in open paper bags, folded envelopes, or folded and pressed envelopes to simulate damage sustained during storage and shipping. We confirmed our findings using tests on seeds from capitula that were initially tested in New Zealand and then shipped to the USA and tested again after transport and inspection.

Materials and Methods

Study species. The musk or nodding thistle, *Carduus nutan*s, is invasive in North and South America, New Zealand, Australia, and Southern Africa. *C. nutans* is propagated only by seed. A single dispersal unit consists of a seed (of the achene type), and a pappus structure which increases drag. In this study, the seeds had an average mass of 2.5 mg (s.e. 0.05 mg; n=309) and were approximately 4 mm long by 1.5 mm in diameter. One capitulum can contain on average ca. 400 seeds (Sezen 2007), and individual plants can produce up to 7,000 (McCarty 1982) or 12,000 seeds (Jongejans et al. 2008a).

Capitulum collection. The thistle capitula for this experiment were harvested from several naturally occurring populations in Central Pennsylvania from 2002-2006, between late June and late July (18 July 2002, 28 July 2003, 30 June 2004, 6 July 2005, 11 July 2006). Capitula were carefully stored to prevent compression.

Packaging treatments. In order to examine the effects of packaging and shipping on terminal velocity measurements collected in the lab, individual capitula were randomly assigned to one of three treatment categories in March 2007: control, envelope, and pressed. There were 25 capitula for each combination of treatment and age (except for 2005, which had 20 control, 21 envelope, and 21 pressed, because fewer capitula were collected in that year). The control capitula were left in open paper bags. The capitula in the envelope category were placed in an envelope and tightly folded and put inside a larger envelope, thus mimicking the tight packaging conditions a capitulum might endure during shipment or space saving storage. The capitula in the pressed category were subjected to the same conditions as the envelope category, with the addition of being crushed with a 12.7 kg weight for at least 15 minutes. The weight was equally distributed to all sections of the envelope to ensure uniform damage to all the enclosed capitula. The pressed category mimics shipping mishandling and tight storage conditions.

Measurements.

Terminal velocity measurements. Each capitulum was dissected in the laboratory. One dispersal unit from each capitulum was chosen at random (using a grid and a chart of random coordinates) for analysis. This was done so that each seed could be analyzed independently, rather than being nested within capitulum of origin. The terminal velocity of each selected dispersal unit was determined by measuring the time seeds took to drop 1.17 m through the still air of an enclosed cardboard tube with an internal diameter of 7.48 cm. The tube had a 10 cm high transparent, plastic viewing shield attached at the top, and two transparent, plastic windows at the bottom: one to shine a light through and one for viewing the dispersal unit as it reached the ground. Manual timing with a digital stopwatch (accuracy 0.01 sec) began after the seed had dropped through the clear plastic shield. Plumed seeds reach terminal velocity quickly (Sheldon & Burrows 1973), and reasonable accuracy in terminal velocity measurement can be achieved when the drop distance is greater than or equal to the terminal velocity squared (Greene & Johnson 1990). None of the terminal velocity measurements were large enough to require a greater drop distance than that provided by the tube used. For each dispersal unit, terminal velocity measurements were repeated until two similar times were obtained and averaged as the drop time (usually the first two drop times were similar enough, i.e. within 0.1 seconds). A tenth of a second represents an error in terminal velocity measurements of 5% or less. The terminal velocity of each dispersal unit was calculated by dividing the timed drop distance by the average drop time.

Pappus and seed measurements. Pappus and seed characteristics were measured after terminal velocity drops to prevent any handling damage to the plume from affecting terminal velocity values (due to the low terminal velocities of the seeds, pappi were not damaged by dropping). Pappus width was measured at the widest point of the pappus and at the width perpendicular to the maximum width with digital callipers (accuracy 0.1 mm). Plume area was determined by assuming that the shape of a pappus is a hollow cone and by calculating the projected area of the cone base as the area of a circle with a diameter of the average pappus width (Meyer & Carlson 2001). Each seed that was used to calculate terminal velocity was weighed to an accuracy of 0.1 mg. Wing loading was calculated as seed mass divided by plume area. The maximum length of the pappus filaments, from the point of attachment to the seed to the top, was measured. The number of filaments in the pappus was counted to obtain a measure of the density of filaments in each pappus. Qualitative pappus damage was also recorded. The most common pappus abnormalities were pappi that were all bent in one general direction, curly or frizzy filaments, or pappi that had gaps where filaments were missing.

Capitulum measurements. The number of dispersal units (seeds still attached to their pappi) was tallied for each dissected capitulum; fewer intact units reduce seed availability for terminal velocity measurements. Maximum capitulum diameter and florivory by the biocontrol agent *Rhinocyllus conicus* (quantified by the number of larval cysts per capitulum) were also determined, as these factors have been shown to increase and decrease the number of seeds produced, respectively (Sezen 2007).

Shipping treatment validation. To validate that the pressed envelope packaging treatment is indicative of shipping conditions, capitula were shipped from New Zealand to the USA. Seeds from these capitula were assessed for terminal velocity before and after shipment. Capitula were collected from two sites on the same farm in New Zealand (site 1: 40°12.744' S, 175° 42.730' E; site 2: 40° 12.988' S, 175° 42.490' E). Capitula were placed in separate paper bags, which were all packaged in a plastic envelope. In New Zealand, seed terminal velocities were measured 84 days after collection. Ten dispersal units (seeds with pappi attached) were sampled from each capitulum and one was chosen randomly for measurement. Seeds were dropped down a 137 cm tall transparent tube of 12 cm diameter, but timing began after seeds had fallen 37 cm to ensure terminal velocity had been reached. The capitula in individual envelopes were then mailed to the U.S.A. When the capitula reached the USA the package was mailed twice more for import inspections. On final arrival, the capitula were completely dissected and one seed was selected randomly from the available remaining dispersal units for terminal velocity measurement. All seeds measured for terminal velocity were also weighed and pappus width and length were recorded. The number of intact dispersal units, capitula diameter, attack by *R. conicus*, and developmental stage of capitula were also quantified.

Data analysis.

Terminal velocity. The effects of packaging treatment and storage duration on seed terminal velocity were evaluated using ANCOVAs with the number of cysts as a covariate (Sokal & Rohlf 1995). Terminal velocity values were log-transformed to increase normality. Storage duration was treated as a continuous variable in all analyses in order to determine whether there was an overall effect of this treatment on the response variables. Generalized linear models (GLMs) were used to determine which differences between treatment means were significant (Crawley 2007). A GLM was used to determine whether plume area, maximum filament length, and filament number were significant explanatory variables for terminal velocity. The square root of wing loading was also assessed as an explanatory variable for terminal velocity with a regression analysis.

Quantitative pappus and seed characteristics. ANCOVAs were used to examine the effects of packaging treatment and storage duration on log-transformed plume area, seed mass, log-transformed wing loading, and filament number using the number of cysts in each capitulum as a covariate to determine how these factors affected seed morphology. The directions of these effects were examined using GLMs.

Qualitative pappus characteristics. GLMs with binomial error distributions were used to determine whether presence/absence measures of qualitative pappus damage (bent, curly, or frizzy filaments or pappi containing gaps) were affected by packing treatments, storage duration, or cysts (Crawley 2007). GLMs with binomial error distributions were also used to determine whether the presence of any one of these qualitative pappus damage assessments was affected by packing, storage, or cysts (Crawley 2007). ANOVAs were used to determine whether the presence of any qualitative measure of pappus damage (bent, curly, or frizzy filaments and pappi containing gaps) affected log-transformed terminal velocity, log-transformed plume area, or the number of filaments per pappus. To examine how the presence of any of these qualitative measures of pappus damage affected the number of dispersal units per capitulum we used a GLM with a quasi-poisson error distribution, because dispersal units were significantly non-normal, over-dispersed, and included many low values.

Capitulum characteristics. GLMs were used to determine the effects of capitulum diameter and collection year on the number of cysts per capitulum in this study. A GLM using a quasi-poisson error distribution was also used to examine how packaging treatment, storage duration, and the number of cysts affected the number of available dispersal units in each capitulum. Dispersal units were also used as a covariate in an ANOVA with packing treatment, storage duration, and cysts to determine whether this variable directly explained any variation in terminal velocity measurements.

Shipping treatment validation. Paired Student's t-tests were used to determine the significance of differences between terminal velocity measurements, plume area, seed mass, and wing loading before and after shipping from New Zealand to the USA. Confidence intervals (95%) were also constructed to compare the difference in terminal velocity values between the control and pressed treatment in the US packing experiment and the difference between terminal velocity values of the New Zealand seeds before and after shipping.

Results

The relationships between the variables that were assessed for their potential impact on terminal velocity are summarized in Figure 1. Terminal velocity, plume area, number of filaments, and number of dispersal units varied between the open, envelope, and pressed treatments (Fig. 2). Storage duration had no clear overall linear effects on these seed characteristics, although significant differences between years did occur.

Terminal velocity. The ANCOVA model showed that packaging treatment had a significant impact on terminal velocity ($p<0.001$; Table 1). The average terminal velocity of the pressed treatment was significantly higher than the averages for the control and envelope treatments (i.e. seeds from pressed capitula fall more quickly and would lead to an underestimation of dispersal distances) ($p<0.001$; Fig. 2A). No overall linear effect of storage duration on terminal velocity was apparent, even though when it was included as a factor (rather than as a continuous variable) there were significant differences in average terminal velocity values between collection years (Table 1; Fig. 2B). Maximum filament length was not a significant predictor of terminal velocity when combined in a GLM with plume area and filament number ($p=0.336$), so further analysis focused on plume area, wing loading, and filament number as explanatory variables for terminal velocity.

Plume area, seed mass, and wing loading. Plume area per dispersal unit decreased with increasingly tight storage conditions: control > envelope > pressed (Table 1; Fig. 2C). However, there was no overall increase or decrease in plume area with storage duration (Table 1; Fig. 2D). Seed mass was not affected by the main effects of packing treatment ($p=0.664$) or storage duration ($p=0.111$). The square root of wing loading (seed mass divided by plume area) was a significant predictor of terminal velocity ($p<0.001$). Packing treatment had a significant effect on wing loading ($p<0.001$), but storage duration was not significant ($p=0.058$).

Filament number. Pappus damage was quantitatively assessed by recording the number of filaments on each pappus. The number of filaments was significantly negatively related to terminal velocity measurements ($p<0.001$). Packaging treatment had a significant negative effect on the number of filaments ($p<0.001$). This was mediated by a significant reduction in pappus filaments for the pressed treatment compared to the control and envelope treatments (Fig. 2E). However, the number of filaments in each pappus stayed broadly constant with storage duration (Fig. 2F).

Qualitative pappus damage. Pappus damage was also assessed qualitatively. The number of pappi with gaps differed significantly between the packaging treatments (Fig. 3); most other effects were marginal (Fig. 3), and qualitative pappus damage did not affect seed terminal velocity ($p=0.43$), plume area ($p=0.37$), or the number of dispersal units ($p=0.56$). The number of filaments per pappus, on the other hand, was significantly related to qualitative pappus damage observations ($p=0.001$).

Available dispersal units. Increasingly tight storage conditions reduced the number of available dispersal units by separating seeds from their pappi when only packing treatment was considered (Fig. 2G). When storage duration and cysts were included in the model the effect of the envelope treatment was not significant ($p=0.132$), while the pressing treatment still was highly significant ($p<0.001$; Table 2). The number of dispersal units per capitulum appeared to increase with storage duration when this was the only variable considered (Fig. 2H), but storage duration was not a significant factor when packaging and cysts were included in the GLM as well ($p=0.923$; Table 2). Thus contrary to expectations, the number of available dispersal units, which affects the choice of units for testing, did not explain a significant amount of variance in terminal velocity values in this study ($p=0.617$).

Cysts. The number of cysts per capitulum varied significantly between collection years ($p<0.001$). Larger capitula also contained more cysts than smaller capitula ($p<0.001$). Cysts per capitulum had a significant positive influence on terminal velocity measurements ($p<0.001$) and on wing loading ($p<0.001$), most likely mediated by the decrease in plume area ($p<0.001$); there was no significant main effect of cysts on seed mass ($p=0.140$). At the same time, as the number of cysts increased, the number of pappus filaments decreased ($p=0.024$). Number of cysts was not a significant factor affecting the presence of qualitative pappus damage ($p=0.389$). Cysts did not significantly affect number of dispersal units as a main effect ($p=0.253$; Table 2), but there was a significant negative interaction between storage duration and cysts ($p=0.023$; Table 2).

Shipping trial. To validate that our pressed packaging treatment was comparable to shipping and to assess the actual effect of shipping on terminal velocity estimates, terminal velocity measurements of seeds from New Zealand were taken at the source (Jongejans et al. 2008a) and then capitula were shipped to the United States for additional terminal velocity measurements. The measured terminal velocity of seeds after shipping was significantly greater than the velocities measured at the source (Fig. 4, $p<0.001$). The 95% confidence interval for the difference between terminal velocity values for the United

States control and pressed treatments was 0.048 - 0.191 m s^{-1} with a difference between the means of 0.120 m s^{-1} which overlaps partly with the 95% confidence interval for the difference in terminal velocity values before and after shipping (0.152 - 0.334 m s^{-1}) with a mean of 0.243 m s^{-1}. Differences in absolute terminal velocity values between New Zealand seeds before shipping and US controls were due to the fact that the New Zealand seeds were significantly lighter ($p<0.001$); their plume areas were not significantly different. Plume area was significantly reduced by shipping ($p<0.001$), but seed mass was not different before and after shipping ($p=0.094$). As a consequence, wing loading increased significantly after shipping ($p=0.001$).

Discussion

The use of existing collections for terminal velocity measurements could save time and money for biogeographic studies linking demography to dispersal, while providing the possibility of examining changes in dispersal ability over time. Our results show that storing capitula in envelopes did not significantly increase seed terminal velocity values unless the envelopes were compressed. Therefore, carefully stored capitula collections may be used for terminal velocity measurements without the risk of artificial increases in terminal velocity. Storage of capitula for one to five years did not result in an overall trend in terminal velocity values, so no degradation in usefulness of stored capitula is expected within this time period. However, as an instantaneous application of pressure can irrevocably damage stored seeds, it is advisable to measure terminal velocities as soon as possible after collection.

Capitula that have been shipped through the post for terminal velocity measurements or that are known to have been compressed should be used with caution. Storage compression can be a serious problem, and we found that international shipment and import inspection in a non-rigid container can double average increases in terminal velocity measurements in comparison to the compression treatment, likely due to additional compression of capitula during shipment. In the case of capitula that have been damaged by compression, terminal velocity measurements can be scaled to take damage into account. This could be accomplished by collecting a sample of similar seeds and measuring the terminal velocity of half the seeds without compression, and treating the other half in a similar way to the previously collected seeds. This of course only approximates the actual damage experienced by the seeds of interest, but it does give a good indication of how sensitive the terminal velocity of particular seeds is to compression.

Changes in terminal velocity caused by compression and shipment in this study were mediated by pappus damage. Decreases in plume area increased wing loading by reducing drag produced by seeds. Reductions in filament number also reduced drag by affecting the total projected area of filaments in pappi, which is an alternative method to calculate plume area than that used in this study (Greene & Johnson 1990). While differences in qualitative pappus damage assessments between the control and pressed packing treatments were marginally significant ($p<0.1$) at the most, similar damage assessments could be useful in other studies.

Although this study was not designed to examine the effects of florivory on seed terminal velocity and morphology, the number of *Rhinocyllus conicus* cysts per capitulum was a significant covariate in several analyses. To our knowledge, this is the first time that a biocontrol agent has been implicated in a reduction in wind dispersal capability. We have conducted a separate study to directly examine these effects, which will provide further insights into how *R. conicus* influences *C. nutans* dispersal (K. M. Marchetto unpublished data).

One potential caveat to the shipment validation results is the use of different apparati for measuring terminal velocity in the USA and New Zealand. The two main concerns were the length of terminal velocity measurement tube used and a potential build up of static electricity on the plastic New Zealand tube. However, we are confident that all terminal velocity measurements had low associated error, and high relative humidity values during terminal velocity drops (mean 69% s.e. 0.12) resulted in low influence of static electricity (less than 30% would be a problem (Vinson & Liou 1998)).

An additional concern is that seed drying within the first few days or weeks of seed storage could cause a difference in seed mass, which would cause later terminal velocity measurements taken in the lab to be lower than those experienced in the field. Unfortunately, the time consuming nature of terminal velocity measurements and capitula dissections posed a logistical constraint on sample processing. Nonetheless, seeds that have passed an initial drying period are still useful for the determination of packaging and shipment effects on relative terminal velocities, and for the effects of storage time on pappus structures.

Our results have strong ramifications for a wide variety of spatial plant ecology issues such as species spread rates (Neubert & Caswell 2000; Skarpaas & Shea 2007; Jongejans *et al.* 2008a), population connectivity (Soons *et al.* 2005), containment of transgenic species (Williams et al. 2006), extinction risk under climate change scenarios (Thomas et al. 2004) and mechanistic metapopulation models (Hanski 1994). For any of these types of studies, incorrect terminal velocity information could lead to inaccurate predictions, which in turn could greatly reduce the effectiveness of management strategies. Even moderate increases in terminal velocity due to compression or shipment could cause substantial under-estimates of dispersal, since spread rates calculated using a WALD (inverse Gaussian) mechanistic dispersal model, for example, are very sensitive to terminal velocity (Skarpaas & Shea 2007). Unbiased estimates of terminal velocity for seeds that have been stored or shipped are also necessary for studying species invasions in a biogeographic context (Hierro et al. 2005). Terminal velocity values have been found to be lower in *C. nutans*' invaded range (Jongejans et al. 2008a), which suggests that this may be true for other species with cosmopolitan distributions. Given the retention of stored seed collections, seed terminal velocity values from transcontinental demography studies could be used or rescaled to understand differences in dispersal and spread between native and invaded ranges without additional field studies cf. (Hinz & Schwarzlaender 2004).

In conclusion, the way in which seeds are stored and shipped can cause a significant increase in terminal velocity measurements through damage to dispersal structures. These differences can affect any models that use terminal velocity as a parameter, including rates of invasive spread, extinction risks under climate change, or expected patch occupancy and metapopulation persistence. With the advances being made in the field of mechanistic spatial plant ecology, we expect that many more of these types of studies will be carried out in the future. New research will doubtless involve proper storage and shipment of capitula in rigid containers. However, seed collections from past transcontinental demographic studies may still be useful if the effects of packaging can be accounted for.

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Table 1: ANCOVA models for log-transformed terminal velocity, log-transformed plume area, and filament number.

		Terminal velocity (m/s)			**Plume Area (mm^2)**			**Filament number**		
	df	**MS**	**F**	**P**	**MS**	**F**	**P**	**MS**	**F**	**P**
Packing treatment	2	1.21	10.63	0.000***	7.53	15.43	0.000***	7526	7.84	0.000***
Storage duration	1	0.34	2.93	0.088	0.51	1.05	0.306	1484	1.55	0.215
Number of cysts	1	5.23	45.77	0.000***	13.72	28.11	0.000***	4915	5.12	0.024*
Residuals	304	0.11			0.49			961		

Variation in characteristics of *Carduus nutans* seeds was explained by the main effects of packaging treatments (control, envelope, or pressed) and storage duration in years with the number of *Rhinocyllus conicus* cysts per capitulum as a covariate. None of the interactions were significant in these models. * p<0.05, ** p<0.01, *** p<0.001

Table 2: Generalized linear model (GLM) for the number of dispersal units per capitulum.

	Estimate	**Standard Error**	**P value**
Envelope treatment	-0.203	0.134	0.132
Pressed treatment	-0.919	0.169	0.000***
Storage duration (S)	0.005	0.047	0.923
Number of cysts (C)	-0.073	0.064	0.253
S*C	-0.071	0.031	0.023*

The number of intact dispersal units (*Carduus nutans* seeds attached to pappi) were modelled as a function of packaging treatment (envelope or pressed, compared to a control treatment), storage duration, and the number of *Rhinocyllus conicus* cysts in a capitulum. All interactions, except the storage duration x cysts number interaction, were not significant and were omitted from the model. * p<0.05, ** p<0.01, *** p<0.001

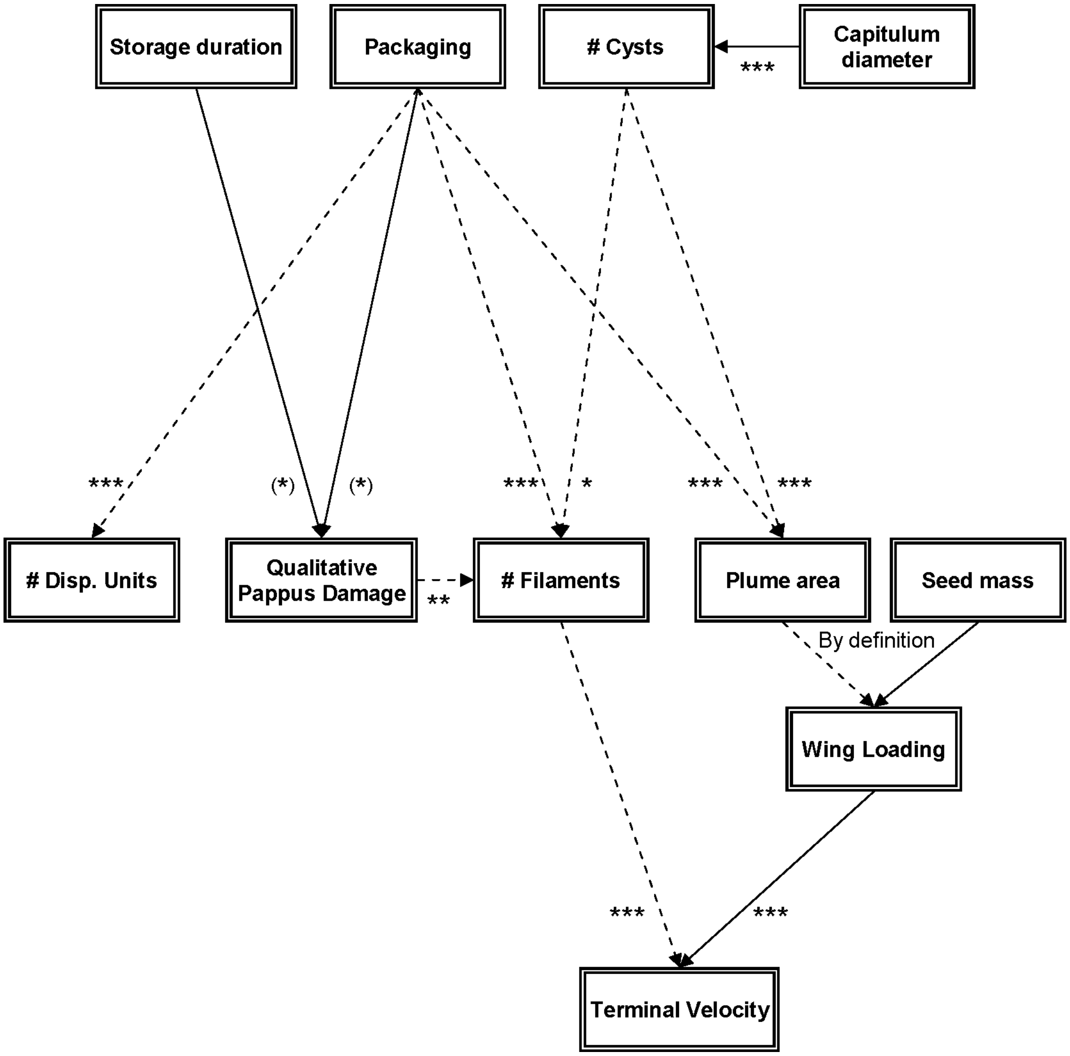

Figure 1: Scheme of factors that affect terminal velocity directly or indirectly.
The diagram summarizes how storage duration, packaging treatment, and number of cysts indirectly affect terminal velocity via other linked variables. Solid lines represent positive effects and dashed lines represent negative effects. Wing loading equals seed mass divided by pappus width. (*) $p<0.1$, * $p<0.05$, ** $p<0.01$, *** $p<0.001$

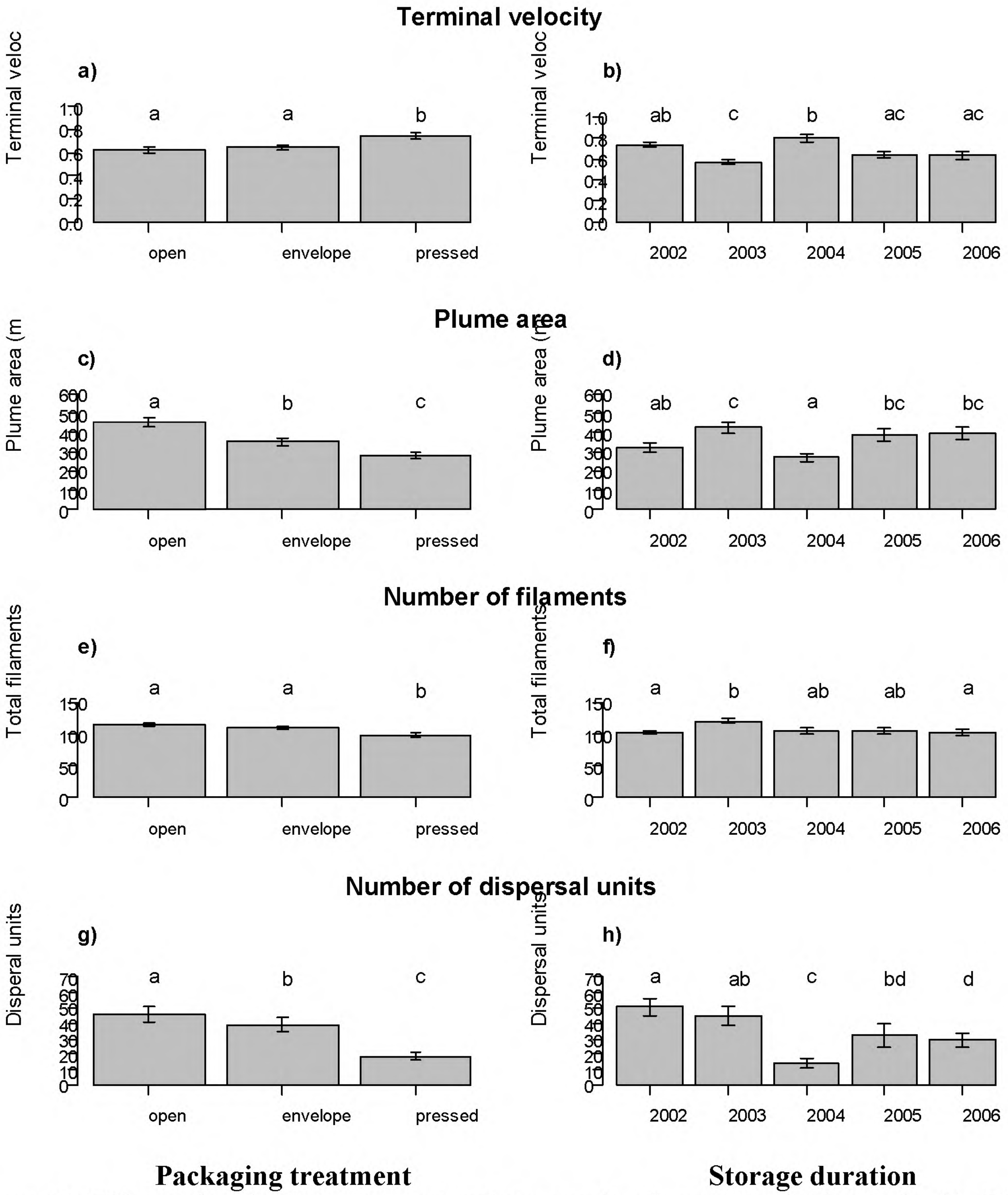

Figure 2: Effects of packaging treatment and storage duration on terminal velocity (A, B), plume area (C, D), number of filaments (E, F), and number of dispersal units (G, H). Mean and standard errors are given for *Carduus nutans* dispersal units from capitula placed in an open paper bag, inside folded paper bags in an envelope, or inside folded paper bags in envelopes that were pressed with a 12.7 kg weight for at least 15 minutes. Capitula were collected from natural populations in Central Pennsylvania, USA in the summers of 2002-2006. Within a panel bars sharing the same letter were not significantly different according to Tukey HSD tests (A-F) and GLMs (G-H).

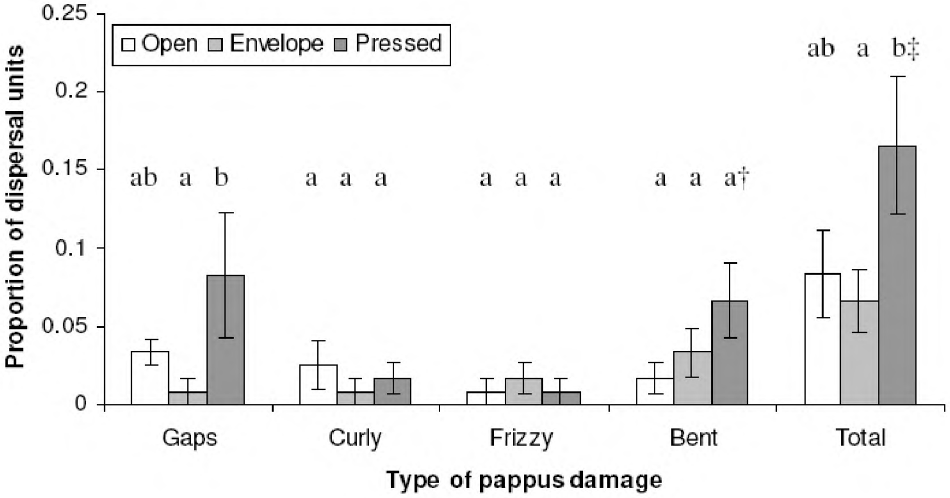

Figure 3: Average numbers of damaged pappi for each packaging treatment.

Average numbers (and standard errors across years) of pappi with gaps in the plume, curly pappi, frizzy pappi, bent pappi, or any of these types of damage are shown for *Carduus nutans* seeds from capitula placed in an open paper bag (N=120), inside folded paper bags in an envelope (N=121), or inside folded paper bags in envelopes that were pressed with a 12.7 kg weight for at least 15 minutes (N=121). Different letters signify significant ($p<0.05$) differences.

† The p value for the difference from the open packaging treatment was 0.074.

‡ The p value for the difference from the open packaging treatment was 0.056.

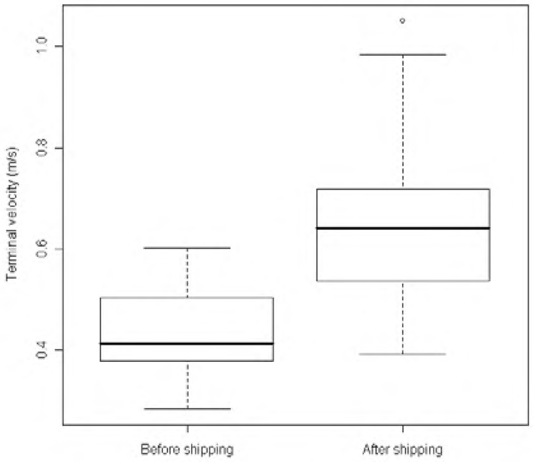

Figure 4: Box plots of measured terminal velocity values before and after shipping capitula.

Terminal velocity measurements were taken for one dispersal unit per capitulum in New Zealand, then capitula were shipped to the United States and different dispersal units from the same capitula were measured for terminal velocity.