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Plant Spatial Arrangement Affects Projected Invasion Speeds of Two Invasive Thistles

Katherine M. Marchetto[1*], Eelke Jongejans[2], Katriona Shea[1], and Scott A. Isard[3]

[1]Department of Biology and IGDP in Ecology, 208 Mueller Laboratory, The Pennsylvania State University, University Park, PA 16802, USA
[2]Department of Experimental Plant Ecology, Radboud University Nijmegen, Heyendaalseweg 135, 6525 AJ Nijmegen, The Netherlands
[3]Department of Plant Pathology, 205 Buckhout Lab, The Pennsylvania State University, University Park, PA 16802, USA

* Communicating author: E: kam5012@psu.edu T: +1-814-865-7912
F: +1-814-865-9131

Abstract

The spatial arrangement of plants in a landscape influences wind flow, but the extent that differences in the density of conspecifics and the height of surrounding vegetation influence population spread rates of wind dispersed plants is unknown. Wind speeds were measured at the capitulum level in conspecific arrays of different sizes and densities in high and low surrounding vegetation to determine how these factors affect wind speeds and therefore population spread rates of two invasive thistle species of economic importance, *Carduus acanthoides* and *C. nutans*. Only the largest and highest density array reduced wind speeds at a central focal thistle plant. The heights of capitula and surrounding vegetation also had significant effects on wind speed. When population spread rates were projected using integrodifference equations coupling previously published demography data with WALD wind dispersal models, large differences in spread rates resulted from differences in average horizontal wind speeds at capitulum caused by conspecific density and surrounding vegetation height. This result highlights the importance of spatial structure for the calculation of accurate spread rates. The management implication is that if a manager has time to remove a limited number of thistle plants, an isolated thistle growing in low surrounding vegetation should be targeted rather than a similar size thistle in a high density population with high surrounding vegetation, if the objective is to reduce spread rates.

Introduction

A spatial perspective is important for the study of plant ecology, because plants have a limited capability to move during most life cycle stages (Harper 1977, Bonan 1993, Dieckmann et al. 2000). Plant migration via seeds affects the spatial and genetic structure of populations, metapopulation dynamics, and invasion speeds (Cain et al. 2000, Nathan and Muller-Landau 2000, Levin et al. 2003, Trakhtenbrot et al. 2005, Skarpaas and Shea 2007, Jongejans et al. 2008b). Many studies have addressed the roles of environmental factors on seed dispersal kernels and spread (Nathan et al. 2002b, Soons et al. 2004a, Soons et al. 2004b, Jongejans et al. 2007, Greene et al. 2008, Soons and

Bullock 2008, Wichmann et al. 2009). Dispersal is best understood for homogeneous environments (Soons et al. 2004a, Skarpaas and Shea 2007, Jongejans et al. 2008a, Soons and Bullock 2008), but there is growing recognition that increasing our understanding of seed movement and population spread in heterogeneous environments is an important next step (With 2002, Buckley et al. 2005, Hastings et al. 2005, Harris et al. 2009). For example, additional research has been called for to addresses the effects of landscape structure on the spread of invasive species (With 2002).

Spatial structure is known to have important effects on invasive spread (Hastings et al. 2005). The spread rate of an invading population can depend on the type of habitat it is colonizing (Buckley et al. 2005) or the spatial distribution of disturbance (Bergelson et al. 1993). In addition, invasive species that modify soil microbial communities to benefit themselves can under certain conditions increase their spread through such positive feedback mechanisms(Levine et al. 2006).

Dispersal vectors can also be greatly influenced by spatial structure (Jordano et al. 2007, Greene et al. 2008, Anderson et al. 2009). For instance, the vegetation surrounding a wind dispersed plant can affect wind conditions and seed dispersal distances (McEvoy and Cox 1987, Lowry and Lowry 1989, Nathan et al. 2002a). Dense plant growth reduces wind speeds within canopies, changing the wind profile (Lowry and Lowry 1989). This effect leads to greater dispersal distances from isolated trees in grasslands than from trees in forests (Nathan et al. 2002a). For the same reason, mowing around plants to reduce surrounding vegetation height increases seed transport (McEvoy and Cox 1987). In addition to their effects on wind speed, dense foliage can also intercept seeds, physically preventing seeds from traveling further (Bullock and Moy 2004).

The influences that differences in wind speed caused by different vegetation elements (e.g. conspecifics or other surrounding vegetation) may have on population spread rates of wind dispersed invasive species are unknown. Here, we examine the effects of differences in conspecific density and surrounding vegetation height together on wind speeds, and simulate population spread of two wind dispersed species from varying source environments. Understanding the effects of these factors on invasive spread has the potential to inform management decisions. For instance, optimal management strategies depend not only on plant demography under different growth conditions, but also on expected spread rates (Menz et al. 1980, Taylor and Hastings 2004, Shea et al. 2010 in press). In addition, management choices could reduce spread rates by prioritizing the removal of plants most likely to produce seeds that will travel furthest (Buckley et al. 2005, Harris et al. 2009).

The purpose of this study was to examine how differences in horizontal wind speed at seed release height caused by surrounding vegetation height and different numbers and densities of conspecifics affect projected population spread rates for two wind dispersed species of invasive thistles, *Carduus acanthoides* L. and *Carduus nutans* L. (Asteraceae). Taller surrounding vegetation, each addition of neighbors, each increase in neighbor density, and lower capitulum heights were predicted to reduce wind speeds at a center focal thistle plant. Increasing numbers and densities of *C. acanthoides* individuals were expected to lower wind speeds at the focal thistle plant more than identical groupings of *C. nutans* due to greater branching in *C. acanthoides*. It was hypothesized that thistle spatial arrangement would affect modeled population spread rates. In order to address these hypotheses, wind speed measurements were taken at capitulum height at a central focal thistle plant in arrays of potted thistles of different sizes and densities of either *C. acanthoides* or *C. nutans* in unmown or mown grass under a variety of weather conditions.

Materials and Methods

Study species. *C. acanthoides* and *C. nutans* are invasive weeds of Eurasian origin that are of economic concern in North America, as well as other continents (Kelly and Popay 1985, Desrochers et al. 1988). Both species are of particular concern in rangelands and pastures, where cattle keep surrounding vegetation low around the unpalatable thistles, in addition to road sides, abandoned fields, and disturbed sites (Lee and Hamrick 1983, Desrochers et al. 1988). Both species are monocarpic perennials that exist as rosettes until bolting, when they produce long 1-2 m stems. *C. nutans* begins flowering earlier in the season and has a shorter flowering period than *C. acanthoides* (Rhoads and Block 2000).

Description of plots. To evaluate the effect of surrounding vegetation height on wind speed in thistle patches, two square 16 m^2 plots were marked in high and low vegetation in a field at Russell E. Larson Research Farm at Rock Springs (N 40.711° W -77.942°). The centers of each plot were 14.7 m apart. For each vegetation height, wind speeds were measured at the center of the plots to minimalize the effect of local topography. For logistical reasons, the high and low vegetation plots were situated on the toe slope of a hill, parallel to the ridge. The low vegetation treatment was mown to a height of 0.05 m, while the high vegetation was not mown and had an average height of 0.74 m during *C. nutans* measurements and an average height of 0.83 m during later *C. acanthoides* measurements. Surrounding vegetation was dominated by *Arrhenatherum elatius*, *Dactylis glomerata*, *Solidago canadensis*, *and Allium* spp. (Sezen 2007).

Description of thistle plants and experimental patch arrays. *C. nutans* and *C. acanthoides* plants used in this experiment were started in the greenhouse and planted in the field as seedlings in the fall of 2006. In the spring of 2007, 29 *Carduus nutans* and 27 *Carduus acanthoides* plants were potted in round, plastic pots with a diameter of 23 cm. The thistles were sorted into three height categories. Three thistles (one from each height category) were randomly selected as focal plants each measurement day, and placed in the center of the plot. Wind speeds were measured upwind of capitula on these plants, either at the top of the plant or towards the center of the plant. Other thistles were randomly assigned spaces around the focal thistle for each of the multiple thistle arrays. The five array configurations tested were individual thistles and square arrays of 8 or 24 plants spaced either pot to pot (stems 23 cm apart) or 1 m apart around the focal plant (see Fig. 1 for a visual representation of the experimental design). Densities of arrays with 23 cm or 1 m spacing between plants were 18.9 thistles m^{-2} or 1 thistle m^{-2}, respectively. Thistle spacing varies in naturally occurring populations, and densities were chosen to cover a range from an initial invasion to high density, economically damaging populations.

Wind speed measurements. Wind speed was measured at a weather station (Campbell Scientific, Inc., Logan, UT, USA) located at the edge of the boundary between high and low vegetation and with a hotwire anemometer (Extech model 407123, Waltham, MA, USA) located at seed release height. The weather station logged wind speeds every ten seconds from a cup anemometer (R. M. Young Wind Sentry

Anemometers, Campbell Scientific Inc., Logan, Utah) at 2 m to measure background wind conditions. The hotwire anemometer measured wind speeds upwind of one of two capitula positions for each focal plant in each array in either low or high surrounding vegetation: at the top of the thistle and in the center of the thistle. The hot wire anemometer measured wind speed every second, and data were collected for 1 minute at each capitulum height in each array and vegetation height. All wind measurements were taken in the afternoon after 1 pm by which time differential surface heating has generally caused windy conditions and an unstable atmosphere conducive to the spread of seeds (Lowry and Lowry 1989, Dauer et al. 2009). Measurements were not taken during rain, due to equipment constraints. *C. nutans* flowers earlier than *C. acanthoides*, so *C. nutans* sampling days (July 9, 10, 12, 13, 16, 17) preceded sampling days for *C. acanthoides* (July 24 and August 1, 6, 8, 10, 13).

Prevention of seed escape. Both study species are invasive weeds, so efforts were taken to prevent seeds from escaping. *C. nutans* capitula were tightly wrapped in fine pollen bag material. *C. acanthoides* produces smaller, more numerous capitula, so adhesive spray was used to prevent seed release.

Statistical Analysis. Wind speed data were analyzed using linear mixed effects models in R (R Development Core Team 2009). Species, surrounding vegetation height, thistle patch array, and measurement height were used as explanatory variables. Weather station wind speeds were used as a covariate to correct for differences in ambient wind speeds. The day and time of each observation were used as nested random variables due to temporal autocorrelation in the data. Deletion tests were used to choose the minimum adequate model based on the AIC value of each model, using the anova function in R (Crawley 2007). The effects of the array size and density could not be determined directly with the full dataset, because the design was unbalanced (arrays with one thistle have no definable density). To examine whether these attributes had significant effects on wind speeds, the analysis was repeated without data from arrays containing one thistle with density and number of thistles as categorical variables in place of thistle array type.

Population Spread Rate Modeling. The effects of extremes in thistle conspecific density (individual or dense 25 plant arrays) and surrounding vegetation height on thistle dispersal were assessed using the WALD dispersal model (Katul et al. 2005). The model is based on an inverse Gaussian distribution and uses four parameters: wind speed, the instability parameter of the wind speed, seed release height, and seed terminal velocity, to determine the dispersal kernel (Katul et al. 2005). The WALD model is known to provide a good fit to *C. acanthoides* and *C. nutans* dispersal data (Skarpaas and Shea 2007). The instability parameter was calculated as in Jongejans et al. (2008a) as standard deviations of vertical wind speeds were not found to be significantly different for different thistle arrays.

Integrodifference equations for *C. nutans* from Jongejans et al. (2008a) were used to calculate the speed with which each species would invade a homogenous landscape (Neubert and Caswell 2000). A 7x7 projection matrix developed by Jongejans et al. (2008a) was parameterized with demography data collected at the experimental site, with relevant modifications, as described below. These data represent a population of *C. nutans* growing in Pennsylvania, USA, under ideal conditions of low competition (Jongejans et al. 2008a). *C. nutans* demography data was used to for both species so that any differences in projected population spread rates would be due to dispersal parameters only. Estimates of seed production and terminal velocities used in the models came from healthy capitula (K.M. Marchetto et al. unpublished data).

A seasonally integrated dispersal kernel was created by simulating the dispersal of ten thousand seeds, with terminal velocities chosen at random from a log-normal distribution (Jongejans et al. 2008a). Seed release heights were chosen from a uniform distribution bounded by the minimum and maximum capitulum heights recorded in our study, ranging from 0.36-1.00 m for *C. acanthoides* and from 0.55-1.10 m for *C. nutans*. Average wind speeds at these random capitulum heights were chosen using the statistical wind speed model and used to randomly pick release wind speeds based on a log normal distribution. The zero plane displacement (d) of the system, a surface roughness parameter used to adjust for differences in seed release height based on a logarithmic wind profile, was evaluated as 0.35*h, where h equals surrounding vegetation height. Jongejans et al. (2008a) used a zero plane displacement of 0.7*h, but a modification was necessary to fit the horizontal wind speeds at the lowest capitulum heights for *C. acanthoides* in high surrounding vegetation. This difference in zero plane displacement could have been caused by convergence of near-ground wind due to the toe slope location.

Projected population spread rates can be calculated by element by element multiplication (indicated by °, the Hadamard product) of the population projection matrix (**A**) with an equally-sized matrix (**M**) containing the moment generating functions of stage-dependent dispersal kernels (Neubert and Caswell 2000, Jongejans et al. 2008a):

$$\mathbf{H} = \mathbf{M} \circ \mathbf{A} \qquad \text{eqn. 1}$$

The population spread rate (c*) is given by

$$c^* = \min_{w>0}\left[\frac{1}{w}\ln(\rho_1(w))\right] \qquad \text{eqn. 2}$$

where ρ_1 is the dominant eigenvalue of **H**, and w is an auxiliary variable (Lewis et al. 2006). One thousand c* values were simulated for each species and for each permutation of intraspecific density and surrounding vegetation height.

Results

Wind speeds. Wind speeds at the patch level differed for different thistle patch arrays and surrounding vegetation heights (Fig. 2**;** Table 1). Wind speeds in thistle patches with high surrounding vegetation were significantly lower than wind speeds in thistle patches in low vegetation ($p<0.001$, Fig. 2B). Dense thistle patches with 25 thistles had significantly lower wind speeds than single thistles ($p<0.001$, Fig. 2C). Wind speeds were also lower at capitula within the canopy of thistle patches than at the top of thistle patches ($p<0.001$, Fig. 2D). Species was not significant as a main effect ($p=0.389$, Fig. 2A), but it was important in an interaction between species and surrounding vegetation height ($p=0.001$, Table 1). When the data were reanalyzed without the individual thistle arrays, high density thistle patches had significantly lower wind speeds than low thistle density patches ($p<0.001$) but array size (9 or 25 thistles) was unimportant ($p=0.28$).

Population spread rates. For both species, the highest spread rates were calculated for populations with low surrounding vegetation and low thistle density. Respective declines in projected population spread rates (c^*) relative to the case of one isolated thistle in low surrounding vegetation for *C. acanthoides* and *C. nutans* were 22%

and 15% for populations with low vegetation and high thistle density, 63% and 31% for populations with high vegetation and low thistle density, and 72% and 39% for populations with both high vegetation and thistle density (Fig. 3). Note that these c^* values rates were calculated with the same population projection matrix, so differences are entirely due to dispersal characteristics.

Discussion

Our results show that even small wind speed differences caused by conspecific density and surrounding vegetation height can greatly affect projected population spread rates for C*arduus acanthoides* and *C. nutans*. As vegetation height and density are heterogeneous in the field, understanding differences in seed dispersal and spread arising from such structure is critical for calculating accurate spread rate predictions (With 2002, Hastings et al. 2005).

While in general the patterns in the wind speeds we measured followed expectations, there were some notable exceptions. For example, only the thistle patches with the largest number of plants at the highest density had a significant effect on wind speeds at the focal thistle, which were most influenced by patch density. Therefore, low density thistles experience the same horizontal wind speeds as isolated thistles, at least up to the maximum patch size tested. The bushy growth habit of *C. acanthoides* did not lead to main effects of species on wind speed or interactions between species and arrangement. However, *C. acanthoides* plants growing in high vegetation had lower than expected wind speeds, causing a large decrease in population spread rates for *C. acanthoides* populations growing in high surrounding vegetation compared to similar *C. nutans* populations.

Since population spread rates are projected to be lower in populations surrounded by high vegetation, thistle populations growing in pastures where livestock maintain low surrounding vegetation heights around thistles are expected to have higher population spread rates than similar populations growing in, for example, abandoned fields. Therefore, it is critical that land managers do not leave isolated thistles growing in pastures. If reduction of thistle spread is the objective, then it would be a better use of a land manager's time to remove an isolated thistle growing in a pasture with low surrounding vegetation than to remove a similar thistle growing in dense surrounding vegetation. However, note that if reduction of high abundance is desired, the opposite recommendation may pertain. Such management recommendations hinge also on whether control costs are to be calculated per individual plant or per area; search time may make removing isolated plants more expensive per individual than removing plant patches.

A single matrix model representing *C. nutans* individuals growing under ideal, low competition conditions (Jongejans et al. 2008a) was used for all scenarios, so reductions in projected population spread rates due to increasing thistle density or surrounding vegetation height are conservative estimates. Some evidence from other species suggest that prioritizing removal of isolated plants may be a more efficient control strategy if eradication is the model objective, because these plants may have a higher fecundity and potential for growth in the absence of high intraspecific competition (Higgins et al. 2000, Miriti et al. 2001, Grevstad 2005). Several recent studies address the question of how or where to prioritize control efforts (outlying or large patches, juveniles or adults, low or high populations, patches near high human use areas, etc.) and optimal control strategies depend on plant biology, budgetary constraints and invasion history (Higgins et al. 2000, Wadsworth et al. 2000, Shea et al. 2002, Taylor and Hastings 2004, Grevstad 2005, Bogich and Shea 2008). For example, prioritizing the removal of isolated plants may reduce spread for "pulled" invasions, where plants at the invasion front contribute most to spread (Levine et al. 2006). Annual plants, or those with high fecundity such as *C. nutans* and *C. acanthoides*, are good examples of species that tend to exhibit pulled invasions (Levine et al. 2006, Harris et al. 2009). However, long lived perennials or low fecundity plants that modify soil chemistry to benefit themselves are expected to exhibit "pushed" invasions, where spread is driven by more mature individuals or populations (Levine et al. 2006, Harris et al. 2009). For pushed invasions, removing older individuals or dense stands at the core of the invasion may be more useful to control spread (Levine et al. 2006, Harris et al. 2009)

The population spread rates calculated here are high in comparison to other modeling projections for these species (Skarpaas and Shea 2007, Jongejans et al. 2008a), but qualitatively similar to results when both species were modeled with the New Zealand *C. nutans* population growth rate of 2.2 (Skarpaas and Shea 2007), likely because they were based on afternoon wind speeds, which are associated with unstable atmospheric conditions that can enhance seed transport (Lowry and Lowry 1989, Dauer et al. 2009). This use of afternoon wind speeds is justifiable because *C. acanthoides* and *C. nutans* seed release increases with high wind speeds prevalent in the afternoon (Jongejans et al. 2007). The location of the experimental plots on the toe slope of a hill may also have influenced results through a directional bias in wind velocity or possible influence to the wind profile (Smith 1976, Doyle and Durran 2002). While the influence of topography on wind profile could make projected population spread rates quantitatively difficult to generalize to other landscapes, horizontal wind speed results were qualitatively consistent with what one would expect based on current research in terms of the effects of capitulum height and varying canopy density (Lowry and Lowry 1989, Nathan et al. 2002a, Poggi et al. 2004).

In addition to the effects of source plant density on seed dispersal through changes in wind speed, plant density and population history can also affect seed morphology and bimodal dispersal in plant species with heteromorphic seeds. More beaked *Hypochoeris glabra* achenes, which have lower terminal velocities that allow them to travel further by wind dispersal, are produced at low parent densities (Baker and O'dowd 1982). At higher intraspecific densities, a greater proportion of unbeaked achenes are produced, which are more suited to animal vectored dispersal (Baker and O'dowd 1982). In other species, seed heteromorphism in dispersal capacity can occur along a successional gradient, between island and mainland populations, and with population age (Olivieri and Gouyon 1985, Cody and Overton 1996). Heteromorphic seeds occur in species belonging to several plant groups, including members of the Asteraceae and the genus *Carduus* (Imbert 2002). The extent of heterocarpy in *C. nutans* and *C. acanthoides* is unknown, but could influence spread modeling of these species in heterogeneous environments and is a topic for future research.

The models used in this study incorporate heterogeneity of source vegetation, but assume landscape homogeneity. The development of seed dispersal and spread models that incorporate heterogeneity at both the source and landscape scales will be an important direction for future research. At the same time, management could be greatly facilitated by decision making models that incorporate habitat heterogeneity in demography and the action of dispersal vectors (Buckley et al. 2005, Jongejans et al. 2008b, Harris et al. 2009). A further interesting extension of this work would be to determine how differences in wind speeds at different capitulum heights and plant densities interact with other processes to affect dispersal in the landscape. For example, *Rhinocyllus conicus* (a receptacle feeding biocontrol agent, which reduces seed production and increases seed terminal velocities (Shorthouse and Lalonde 1984, Smith and Kok 1984, Sezen 2007, Marchetto et al. 2010a)) is more likely to oviposit on taller *C. nutans* capitula (Sezen 2007), which would normally receive the highest wind speeds. Additionally, fluid dynamics techniques, such as Particle Image Velocimetry, could be used to obtain a more detailed understanding of wind velocity and turbulence at different capitulum positions for isolated thistles and in sparse canopies (Marchetto et al. 2010b in press).

In conclusion, differences in wind speeds at capitula, caused by surrounding vegetation height and conspecific density, can result in large differences in projected population spread rates. Spread models that incorporate greater spatial realism will thus be useful in the study of population dynamics and species management for conservation or invasive species control.

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Table 1: Fixed effects from the minimum adequate linear mixed effects model describing wind speeds measured at focal plants.

	Parameter	Std. Error	DF	P value
Intercept	1.91	0.16	43834	0.000
Ambient wind speed (m/s)	0.36	0.02	4094	0.000
C. nutans species (S)	-0.16	0.18	11	0.389
High surrounding vegetation (V)	-0.77	0.11	1528	0.000
9 plants 1 m apart	-0.01	0.08	1528	0.874
9 plants 23 cm apart	-0.13	0.07	1528	0.079
25 plants 1 m apart	0.01	0.08	1528	0.916
25 plants 23 cm apart	-0.34	0.08	1528	0.000
Capitula inside canopy	-0.25	0.04	4094	0.000
S*V	0.52	0.15	1528	0.001

The reference thistle array type, surrounding vegetation height, and measurement location for this model is a *Carduus acanthoides* patch in low surrounding vegetation with 1 plant and wind speeds measured at the top of the canopy. The day, hour, minute, and second that wind speeds were recorded were used as random nested variables in the model. Ambient wind speeds were measured at a height of 2 m at a nearby weather station.

Figure 1: Visual representation of the experimental design. Plant positions in arrays located in different plots were randomly assigned each measurement day. There were a total of 60 wind speed measurements of 60 seconds each per species per day. Patch arrays consisted of 1 plant or 9 and 25 plant matrices spaced 1 m apart (1 thistle m^{-2}) or with pots touching (18.9 thistles m^{-2}). Wind speeds were measured at capitulum height upwind of capitula at the top of the focal plant, and lower capitula towards the plant center. A tall, a medium, and a short center plant were chosen randomly for each array, to serve as replicates. Flower motifs adapted from S. Yang.

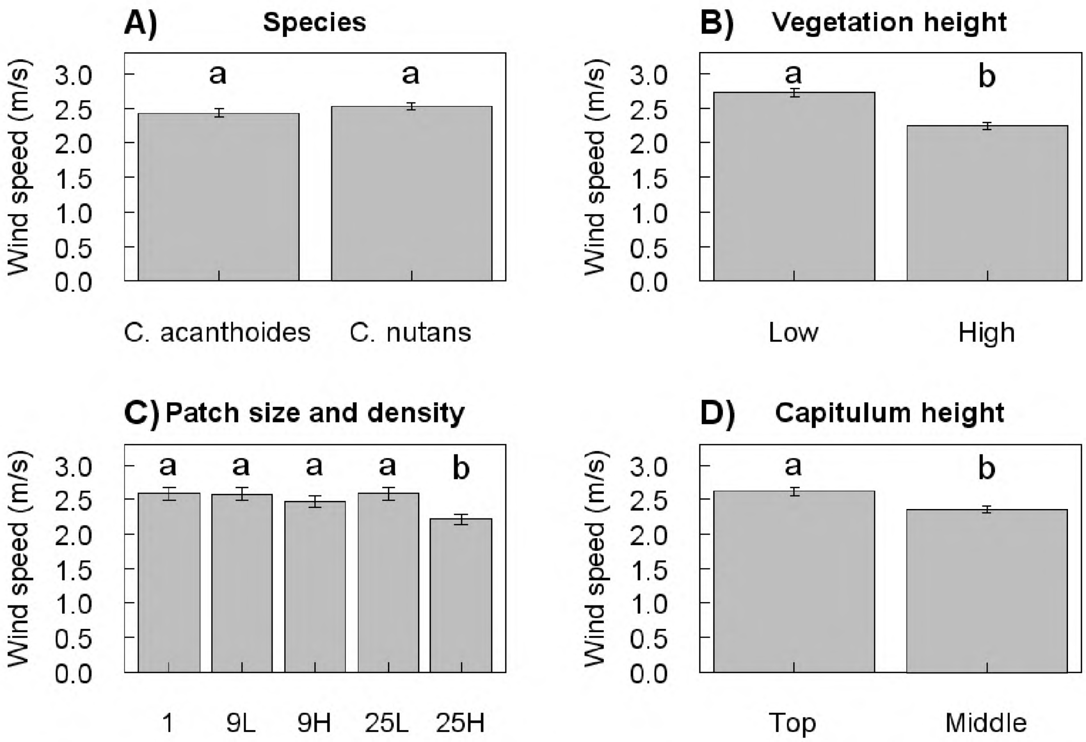

Figure 2: Effects of A) species, B) surrounding vegetation height, C) thistle patch size and density, and D) categorical capitulum height on average wind speeds recorded at capitula. Wind speed values were taken every second and then averaged for one minute measurement intervals for each replicate and each measurement day to obtain standard error bars. Significance levels between treatments are based on the minimum adequate linear mixed effect model with ambient wind speed measured at a nearby weather station as a covariate and measurement day, hour, minute, and second as nested random variables. Measurements taken at *Carduus acanthoides* capitula and *Carduus nutans* capitula given in panel A). The patch size and density categories in panel C) represent arrays with one individual thistle (1), arrays with 9 thistles spaced 1 m apart in a 3 x 3 matrix (9L), arrays with 9 thistles spaced 23 cm apart in a 3 x 3 matrix (9H), arrays with 25 matrices of thistles spaced 1 m apart in a 5 x 5 matrix (25L), and arrays with 25 matrices of thistles spaced 23 cm apart in a 5 x 5 matrix (25H). Arrays with plants 23 cm apart or 1 m apart had densities of 18.9 thistles m^{-2} or 1 thistle m^{-2}, respectively.

Categorical capitulum heights in panel D) represent measurements taken at capitula at the top of thistle canopies or in the middle of thistle canopies.

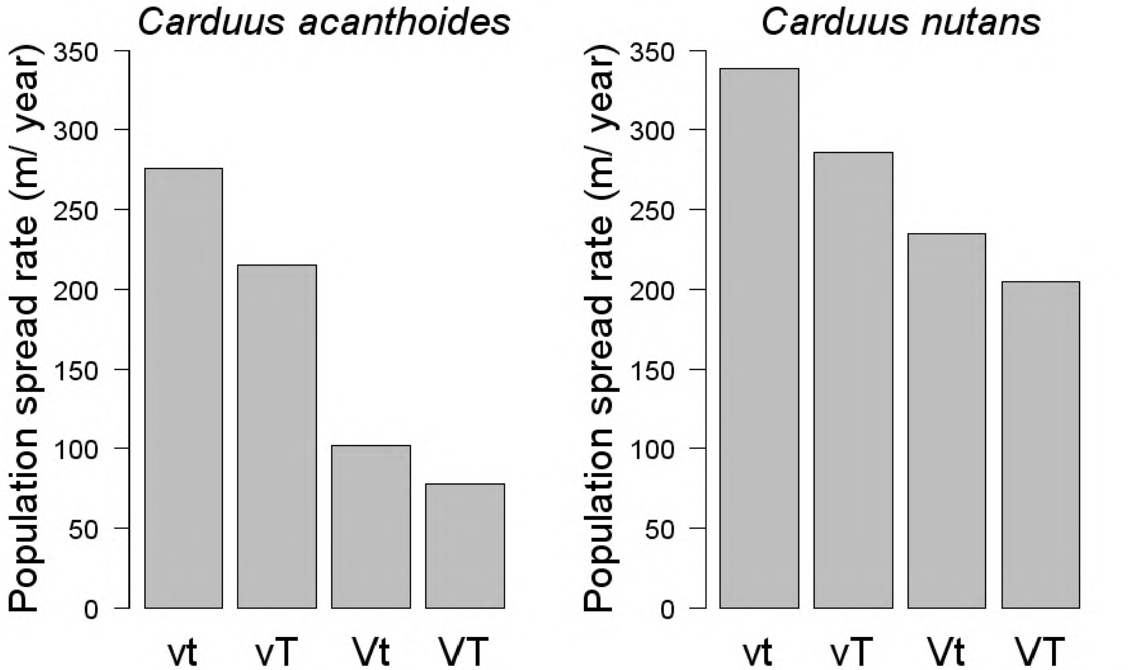

Figure 3: Modeled population spread rates for healthy *Carduus acanthoides* and *Carduus nutans* populations.

Population spread rates for thistles in low surrounding vegetation with low conspecific thistle density (vt), low surrounding vegetation with high conspecific thistle density (vT), high surrounding vegetation with low conspecific thistle density (Vt), and high surrounding vegetation with high conspecific thistle density (VT) were calculated with the same population growth rate for both species representing an experimental population of *Carduus nutans* growing under ideal conditions. Wind speeds were based on empirical results for low vegetation with 1 thistle or 25 thistles at a density of 18.9 thistles m^{-2} (vt or vT), or high vegetation with 1 thistle or 25 thistles at a density of 18.9 thistles m^{-2} (Vt or VT). One thousand population spread rates were calculated to determine median population spread rates.