Appendix A: Detailed description of population spread rate model.

Population spread rates including the effects of cysts on seed production, release, and terminal velocity were determined for two *Carduus nutans* populations in United States and New Zealand populations using coupled integrodifference models, which allow the calculation of a traveling wave speed, c*, for a species invading a homogenous landscape (Neubert and Caswell 2000, Neubert and Parker 2004, Jongejans et al. 2008). Two components are used to calculate the spread rate, a population projection matrix (**A**), and a matrix (**M**) containing the moment generating function for each dispersive stage. The modeling methods were modified from Jongejans et al. (2008) to include a new population projection matrix which also tracks the fates of plants derived from seeds that are not released from the parent plant, inclusion of stochastic seedling establishment probabilities, and the incorporation of functions, based on our new empirical data and wind tunnel trials, for the effects of a range of weevil damage on seed production, release, and terminal velocity.

Population projection matrix. Demographic vital rates for the generation of population projection models came from an experimental population of *C. nutans* from Pennsylvania, United States and a *C. nutans* population along Midland Rd. near Ashhurst, New Zealand (K. Shea, *unpublished data* 2002–2005; Shea and Kelly 1998, Jongejans et al. 2008). The US experiment provided vital rates for plants growing under ideal conditions of low competition and increased resource availability. This experiment is described in detail in Jongejans et al. (2008).

A 12 × 12 matrix was developed based on the 4 × 4 stage structured matrix of Shea and Kelly (1998) and the 7 × 7 matrix used by Jongejans et al. (2008) to include information concerning reductions in seed release caused by cysts (Eq. A.1). The four main stages are: seed bank (SB), small (S), medium (M), and large (L) each divided into three substages: individuals derived from dispersing seeds (D), individuals derived from non-dispersing seeds (ND), and locally surviving individuals (LS). The order of the rows in Eq. 1 corresponds to SB-D, SB-ND, SB-LS, S-D, S-ND, S-LS, M-D, M-ND, M-LS, L-D, L-ND and L-LS from top to bottom. Non-dispersing seeds are those that fail to release from capitula. Parameter definitions are given in Table A1. Seedling establishment probabilities were drawn from beta distributions that included realistic ranges of values from empirical data reported in Peterson-Smith and Shea (2010). The proportion of seeds left after weevil larval feeding (φ) was calculated as a function of the average number of cysts and average capitulum diameter (35.4 mm for US and 14.7 mm for NZ). Proportions of non-dispersing seeds for a range of *R. conicus* cysts came from a statistical model of the number of seeds stuck in *C. nutans* flower receptacles, which failed to release before, during, or after wind tunnel trials and remained after all loose seeds were removed from capitula manually. The proportion of seeds that disperse (δ) was calculated as one minus the fitted model for the proportion of seeds stuck in the capitulum as a function of cysts. All three substage columns are calculated using the same formulae, with different parameter values, so only one column is shown for each main stage class. The dominant eigenvalue of this matrix is the population growth rate (Caswell 2001).

SB Small Medium Large

$$\begin{pmatrix}
0 & \sigma_2\beta_2\pi_2\varphi\nu\delta & \sigma_3\beta_3\pi_3\varphi\nu\delta & \sigma_4\beta_4\pi_4\varphi\nu\delta \\
0 & \sigma_2\beta_2\pi_2\varphi\nu(1-\delta) & \sigma_3\beta_3\pi_3\varphi\nu(1-\delta) & \sigma_4\beta_4\pi_4\varphi\nu(1-\delta) \\
\sigma_1 & 0 & 0 & 0 \\
0 & \sigma_2\beta_2\pi_2\varphi\varepsilon(1-\gamma_3-\gamma_4)\delta & \sigma_3\beta_3\pi_3\varphi\varepsilon(1-\gamma_3-\gamma_4)\delta & \sigma_4\beta_4\pi_4\varphi\varepsilon(1-\gamma_3-\gamma_4)\delta \\
0 & \sigma_2\beta_2\pi_2\varphi\varepsilon(1-\gamma_3-\gamma_4)(1-\delta) & \sigma_3\beta_3\pi_3\varphi\varepsilon(1-\gamma_3-\gamma_4)(1-\delta) & \sigma_4\beta_4\pi_4\varphi\varepsilon(1-\gamma_3-\gamma_4)(1-\delta) \\
\varepsilon_1(1-\gamma_3-\gamma_4) & \sigma_2(1\text{-}\beta_2)(1-\gamma_{32}-\gamma_{42}) & \sigma_3(1\text{-}\beta_3)\rho_{23} & \sigma_4(1\text{-}\beta_4)\rho_{24} \\
0 & \sigma_2\beta_2\pi_2\varphi\varepsilon\gamma_3\delta & \sigma_3\beta_3\pi_3\varphi\varepsilon\gamma_3\delta & \sigma_4\beta_4\pi_4\varphi\varepsilon\gamma_3\delta \\
0 & \sigma_2\beta_2\pi_2\varphi\varepsilon\gamma_3(1-\delta) & \sigma_3\beta_3\pi_3\varphi\varepsilon\gamma_3(1-\delta) & \sigma_4\beta_4\pi_4\varphi\varepsilon\gamma_3(1-\delta) \\
\varepsilon_1\gamma_3 & \sigma_2(1\text{-}\beta_2)\gamma_{32} & \sigma_3(1\text{-}\beta_3)(1-\rho_{23}-\gamma_{43}) & \sigma_4(1\text{-}\beta_4)\rho_{34} \\
0 & \sigma_2\beta_2\pi_2\varphi\varepsilon\gamma_4\delta & \sigma_3\beta_3\pi_3\varphi\varepsilon\gamma_4\delta & \sigma_4\beta_4\pi_4\varphi\varepsilon\gamma_4\delta \\
0 & \sigma_2\beta_2\pi_2\varphi\varepsilon\gamma_4(1-\delta) & \sigma_3\beta_3\pi_3\varphi\varepsilon\gamma_4(1-\delta) & \sigma_4\beta_4\pi_4\varphi\varepsilon\gamma_4(1-\delta) \\
\varepsilon_1\gamma_4 & \sigma_2(1\text{-}\beta_2)\gamma_{42} & \sigma_3(1\text{-}\beta_3)\gamma_{43} & \sigma_4(1\text{-}\beta_4)(1-\rho_{24}-\rho_{34})
\end{pmatrix} \quad \text{(A.1)}$$

Moment generating function. A seasonally integrated dispersal kernel was calculated using the WALD dispersal model developed by Katul et al. (2005) modeled as in Jongejans et al. (2008). See Table A1 for parameter values. The WALD model was used because it has been found to give a good fit to dispersal data from *C. nutans* (Skarpaas and Shea 2007).

Hourly wind speed measurements were collected from State College, Pennsylvania, USA from July–August 1999–2006. Wind speed (U) at seed release height (H) was calculated from wind speed at measurement height (U_m) assuming a logarithmic wind profile:

$$U = \frac{1}{H}\int_0^H \frac{u_*}{K}\log(\frac{z-d}{0})dz \quad \text{(A.2)}$$

where u* is the friction velocity, K is the von Karman constant (0.4), z is height above ground, and following Skarpaas and Shea (2007) the surface roughness parameters d and z_0 are defined as d = 0.7h and z_0 = 0.1h. The friction velocity is defined as:

$$u_* = KU_m[log(\frac{z_m-d}{z_0})]^{-1} \quad \text{(A.3)}$$

where U_m and z_m are the wind speed and height above ground at measurement height. The instability parameter of wind flow was calculated as:

$$\sigma = 2A_W^2 \sqrt{\frac{K(z-d)u_*}{C_0 U}} \qquad \text{(A.4)}$$

where C_0 is the Kolmogorov constant (3.125) and A_w is assumed to be 1.3 for turbulent flow above the canopy (Skarpaas and Shea 2007).

The WALD dispersal model uses wind speed, an instability parameter, terminal velocity (F), and seed release height to determine a dispersal kernel and can be seasonally integrated and marginalized in one dimension (Lewis et al. 2006). The formula is given by:

$$p(r) = (\frac{\xi'}{2\pi r^3})^{\frac{1}{2}} exp(-\frac{\xi'(r-\mu')^2}{2\mu'^2 r}) \qquad \text{(A.5)}$$

where the location parameter, μ, and the scale parameter, ξ, are defined as:

$$\mu' = \frac{HU}{F} \qquad \text{(A.6)}$$

$$\xi' = (\frac{H}{\sigma})^2 \qquad \text{(A.7)}$$

according to Katul et al. (2005). Variation in wind speed over the dispersal season and in terminal velocity values for different seeds can be accounted for by seasonally integrating the WALD model to determine a 2D radial dispersal kernel, *k(r)*:

$$k(r) = \int \int p(F)p(U)p(r)dFdU \qquad \text{(A.8)}$$

where *p(F)* and *p(U)* are the probability density functions of *F* and *U* respectively (Skarpaas and Shea 2007, Jongejans et al. 2008). The mean of the probability density function for terminal velocity was treated as a function of cysts using fitted model output. The kernel can be marginalized to estimate the spread rate in one dimension by simulating a large number (e.g., 10,000) of dispersal distances, *r*, using the seasonally integrated model with associated random angles, α, from a uniform distribution of angles from 0-2π and calculating $x = r \cos(\alpha)$ (Jongejans et al. 2008). The moment generating function is then defined as:

$$M^E(w) = \frac{1}{N}\sum_{i=1}^{N} exp(wx) \tag{A.9}$$

where *w* is an auxiliary variable (Lewis et al. 2006). The moment generating function is then placed in a 12 × 12 matrix (**M**), where values of 1 denote non-dispersing stages. The matrix in Eq. A.10 shows only one main stage class column for each of the three identical substage columns in the full matrix.

$$\begin{pmatrix} 1 & M^E(w) & M^E(w) & M^E(w) \\ 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 \\ 1 & M^E(w) & M^E(w) & M^E(w) \\ 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 \\ 1 & M^E(w) & M^E(w) & M^E(w) \\ 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 \\ 1 & M^E(w) & M^E(w) & M^E(w) \\ 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 \end{pmatrix} \tag{A.10}$$

Spread rate calculation. To calculate the spread rate, the matrix model (**A**) and the moment generating function matrix (**M**) are multiplied element by element using Hadamard normal matrix multiplication to produce a new matrix, $\mathbf{H}=\mathbf{M}\circ\mathbf{A}$ (Neubert and Caswell 2000). The spread rate, c*, can then be calculated by:

$$c^* = \min_{s>0}[\frac{1}{s}\ln(\rho_1(w))] \tag{A.11}$$

where ρ_1 is the dominant eigenvalue of **H**.

Spread rates were calculated for all possible combinations of the effects of *R. conicus* herbivory on seed production, seed release, and terminal velocity for a range of average number of cysts per capitulum ranging from 0–15, to examine which effects were most important in determining the overall calculated spread rates. The effects of *R. conicus* damage on seed release and dispersal were assumed to be the same for the US and NZ populations for capitula of the same size. The mean of the probability density function for terminal velocity was treated as a function of cysts using fitted model output (Table A1). Terminal velocity values from the NZ population came from healthy *C. nutans* capitula without attack by *R. conicus* (Marchetto et al. 2010). Average numbers of cysts per capitulum come from experimental Pennsylvanian US plants (Z. Sezen, *unpublished data*) and naturalized plants near Argyll, NZ (Shea and Kelly 1998). Due to the stochastic nature of the model, median population spread rates generated from ten thousand simulated population spread rates were reported.

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TABLE A1. Definitions of parameter values. Parameters in italics were estimated from a different population (see Jongejans et al. 2008 for details). *Values are given for the average number of cysts for each population. Seedling establishment rates for both the US and NZ populations were chosen from beta distributions. † Seedling establishment rates for the US population had mean 0.2333, alpha 3.5, and beta 11.5. ‡ Seedling establishment rates for the NZ population had mean 0.0194, alpha 0.012, and beta 0.607 for new seeds and mean 0.1847, alpha 1.8, and beta 9.665 from the seed bank.

Population		USA, Pennsylvania, experimental	New Zealand, Midland Rd., natural
Stage class borders:			
Between S and M [cm^2]		16.6	83.1
Between M and L [cm^2]		841	175
Demographic parameters:			
Survival of seed in SB	s_1	*0.2597*	0.0382
Survival of S	s_2	0.2619	0.1164
Survival of M	s_3	0.6761	0.6813
Survival of L	s_4	0.8971	0.7532
Growth of establishing seed to M	g_3	0.2076	0
Growth of establishing seed to L	g_4	0.0911	0
Growth of surviving, not-bolting S to M	g_{32}	0.8028	0.1065
Growth of surviving, not-bolting S to L	g_{42}	0.1268	0.0651
Retrogression of surviving, not-bolting M to S	r_{23}	0	0.3333
Growth of surviving, not-bolting M to L	g_{43}	0.3824	0.6667
Retrogression of surviving, not-bolting L to S	r_{24}	0	1
Retrogression of surviving, not-bolting L to M	r_{34}	0	0
Bolting of surviving S	b_2	0.1932	0.262
Bolting of surviving M	b_3	0.7143	0.9516
Bolting of surviving L	b_4	1	0.9828
Potential seed production by S	p_2	5443	2437
Potential seed production by M	p_3	6150	2776
Potential seed production by L	p_4	12446	3576
Potential seed escaping from floral herbivory	j	0.3238*	0.6952*
New seed entering SB	n	*0.2333*	0.157
New seed establishing seedling	e	mean: 0.2333†	mean: 0.0194‡
Seed from SB establishing seedling	e_1	mean: 0.2333†	mean: 0.1847‡
Dispersal parameters:			
Proportion of seeds that disperse	δ	0.8148*	0.9041*
Geometric mean terminal falling velocity [$m\ s^{-1}$]	F	0.4923	0.4325
Standard deviation of F [$m\ s^{-1}$]	s_F	0.2427	0.1952
Mean release height (mean plant height) [cm]	H	184	57
Vegetation height [cm]	h	50	4
Geometric mean wind speed [$m\ s^{-1}$] at 10m	U	1.7257	3.5365
Standard deviation of U [$m\ s^{-1}$]	s_U	0.728	0.7541