

Optimal management strategies to control local population growth or population spread may not be the same

KATRIONA SHEA,^{1,6} EELKE JONGEJANS,² OLAV SKARPAAS,³ DAVE KELLY,⁴ AND ANDY W. SHEPPARD⁵

¹Department of Biology and Intercollege Graduate Degree Program in Ecology, 208 Mueller Laboratory, The Pennsylvania State University, University Park, Pennsylvania 16802 USA

²Department of Experimental Plant Ecology, Institute for Water and Wetland Research, Radboud University Nijmegen, Heyendaalseweg 135, 6525 AJ Nijmegen, The Netherlands

³Norwegian Institute for Nature Research, Gaustadalléen 21, NO-0349 Oslo, Norway

⁴Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch 8140 New Zealand

⁵CSIRO Entomology, GPO Box 1700, Canberra, ACT 2601 Australia

Abstract. The objective of most pest management programs is to “control” the pest species. However, optimal control of local abundance and population growth may require different management strategies than optimal control of spatial spread. We use coupled demographic–dispersal models to address the relative importance of different management approaches to these two main control objectives for the invasive thistle *Carduus nutans*. The models are parameterized with data from thistle populations in the native (France) and invaded ranges (Australia and New Zealand). We assess a wide range of commonly used management strategies for their absolute and relative impacts on population growth and spread in both invaded-range scenarios.

The projected population growth rate in New Zealand is more than twice that in Australia, while the spread rate is more than four times the Australian value. In general, spread and growth are both most strongly affected by the same life cycle transitions; however, in a few cases certain vital rates disproportionately affect either spread or growth. The transition that represents the contribution of large rosettes in one year to the number of large rosettes in the following year (the large rosette–large rosette transition) in Australia is dominated by reproduction (rather than survival) and hence is relatively more important to spread than to population growth. In New Zealand, the small rosette–small rosette transition is also predominantly dispersal-related. However, establishment of small plants from the seed bank contributes more to population growth than spread, as no dispersal is involved.

The fine-resolution vital-rate-based modeling approach allows us to identify potentially novel optimal management strategies: approaches that reduce microsite availability show promise for reducing both population growth and spread, while strategies that affect dispersal parameters will affect spread. Additionally, the relative ranking of some biocontrol agents shifts depending on whether control of population growth or population spread is the desired outcome and therefore could alter which of the agents are preferred for release in a new area. The possibility of differences in ranked agent effectiveness has been predicted theoretically, but never before demonstrated using field data.

Key words: *Carduus nutans*; demography–dispersal models; integrodifference equations; matrix population models; musk or nodding thistle; native vs. invaded range; optimal management; population growth; population spread; vital rates; Wald analytical long-distance model.

INTRODUCTION

Many management programs for pests and weeds are species-specific, with a stated objective to “control” the problem species. However, “control” can imply a variety of different specific management aims. A majority of studies implicitly or explicitly focus on reducing local population growth rates or density (e.g., Shea and Kelly 1998, Shea et al. 1998); relatively few explicitly state a

spread reduction objective (e.g., Paynter et al. 1996, Bogich and Shea 2008). However, it is not immediately clear whether management strategies to control local abundance and population growth of a species are also most suitable to control its spatial spread. A lack of clarity can significantly hinder management efforts. For example, a longstanding debate on the value of seed feeders as agents for weed biological control likely arises from a poor understanding of differences in the weed control goals relating to reduced spread and population suppression (Harper 1977, Crawley 1989, Paynter et al. 1996, Moran et al. 2004). Prior theoretical work, using simple demographic models and plausible dispersal kernels, has shown that the life history transition with

Manuscript received 23 February 2009; revised 3 September 2009; accepted 9 September 2009. Corresponding Editor: T. J. Stohlgren.

⁶ E-mail: k-shea@psu.edu

the largest potential impact on the population growth rate may indeed not be the life history transition with the largest potential impact on population spread rate (Shea 2004). If such results are common or if differences in impacts are large, managers will have to be very specific about their management aims in order to identify appropriate optimal management strategies.

Unfortunately, experimental assessments of all possible management strategies are prohibitively complex, both in terms of time and logistics. Assessing for different objectives would only add an extra layer of complexity to the issue. An alternative approach is to assess competing management strategies using simple models; at the least this allows triage of the few most promising strategies (Shea et al. 2006) for field-testing. Demographic matrix models have been particularly influential in this area (e.g., Shea and Kelly 1998, McEvoy and Coombs 1999, Mertens et al. 2002, Emery and Gross 2005, DeWalt 2006, Hansen and Wilson 2006). Recently, methods have been developed that allow these demographic models to be coupled to simple models of dispersal, allowing the estimation of spread rates (Neubert and Caswell 2000). These advances clearly have practical importance and can be applied to address spread management of invasive species (Neubert and Parker 2004, Buckley et al. 2005, Bullock et al. 2008) and will be particularly useful in tailoring management to appropriate spatial scales (Pauchard and Shea 2006).

In this paper, we use such coupled demographic–dispersal models to extend this approach to address the relative importance of different management approaches to the two main potential control objectives for the invasive plant *Carduus nutans* (musk or nodding thistle). A range of commonly used management strategies for this species (including biological control and chemical and cultural practices) are tested in demographic matrix models linked to models of seed dispersal, to assess their potential absolute and relative impacts on local population growth rates and spatial spread. The demography and dispersal models are parameterized with *C. nutans* data from populations in its native (France) and invaded ranges (Australia and New Zealand).

METHODS

Carduus nutans L. (Asteraceae) is a monocarpic perennial thistle of Eurasian origin. It has invaded the Americas, New Zealand, Australia, and southern Africa, causing significant economic damage (Desrochers et al. 1988, Popay and Medd 1995, Shea et al. 2005, Allen and Shea 2006). A wide range of approaches is used to manage this species, but the focus of management method comparisons has been on local abundance through suppression of population growth (e.g., Popay and Medd 1995, Shea and Kelly 1998, Huwer et al. 2005, Shea et al. 2006). No work explicitly addresses management impacts on spatial spread, although Kelly and McCallum (1995) raised the point that biocontrol

agents that were ineffective at reducing local density of *C. nutans* could still be effective at reducing spread.

To assess the potential effects of different management strategies on both population growth and spatial spread, we used an approach that combines matrix models of local demography with mechanistic models of seed dispersal. The demographic models are based on data from France in the native range and from New Zealand and Australia in the invaded range (Sheppard et al. 1989, 1994, Shea and Kelly 1998, Shea et al. 2005, 2006, Jongejans et al. 2006, 2008). All three data sets were from sites in sheep-grazed pastures. The French site was at La Cavalerie (44°00' N, 3°08' E), at 787 m elevation, with relatively infertile limestone soil, an average rainfall of 1000 mm/yr and mean summer air temperatures of 20.0°C. The Australian data came from Kybeyan, New South Wales (36°22' S, 149°24' E), at 998 m elevation, with fertile tertiary basalt-based soil, an average rainfall of 690 mm/yr, and mean summer air temperatures of 22.3°C. The New Zealand site was at Midland, Manawatu (40°15' S, 175°43' E), at 200 m elevation, with yellow-gray earths, graywacke (sandstone)-based soil, an average rainfall of 990 mm/yr, and mean summer air temperatures of 16.1°C. Dominant perennial pasture species at the French site included *Lolium perenne* and *Dactylis glomerata*. At the Australian site *Phalaris aquatica* and *Trifolium subterraneum* dominated, while *L. perenne* and *T. repens* were the most common plants at the New Zealand site.

Transition matrix models (Caswell 2001) provide a simple representation of a species' life cycle; each element in such a matrix represents the transition from one life stage to the next. The model can be used to project the dynamics of the population, and various matrix properties have clear biological interpretations. In particular, the dominant eigenvalue, λ , is the projected population growth rate (Caswell 2001), and the elasticities (or proportional sensitivities) indicate the relative contributions of perturbations in the matrix elements to the growth rate (de Kroon et al. 2000).

The structure of the matrix model for *C. nutans* is shown in Table 1. Each of the 16 elements (for example, the L–L transition element, which represents the contribution of large rosettes in one year to the number of large rosettes in the following year) in the 4×4 matrix is a composite of several vital rates. Note that there are several vital rates in most elements and that a vital rate may appear in more than one element. These vital rates have clear biological meanings; for example, σ_4 is the survival of large rosettes. Table 2 lists the definitions of each vital rate (e.g., growth, survival, seed production) as well as the parameters estimated for each population from a variety of sources (summarized in Jongejans et al. 2008).

Dispersal was modeled using the mechanistic Wald analytical long-distance dispersal (WALD) model (Katul et al. 2005, Skarpaas and Shea 2007) using data from the same regions (Jongejans et al. 2008). Again,

TABLE 1. Demographic and dispersal models are coupled and used to assess management strategies.

Demographic model (vital rate-based matrix model)			
Seed bank (SB)	Small (S)	Medium (M)	Large (L)
$\begin{pmatrix} \sigma_1 \\ \varepsilon_1(1-\gamma_3-\gamma_4) \\ \varepsilon_1\gamma_3 \\ \varepsilon_1\gamma_4 \end{pmatrix}$	$\begin{pmatrix} \sigma_2\beta_2\pi_2\varphi\nu \\ \sigma_2(1-\beta_2)(1-\gamma_{32}-\gamma_{42}) + \sigma_2\beta_2\pi_2\varphi\varepsilon(1-\gamma_3-\gamma_4) \\ \sigma_2(1-\beta_2)\gamma_{32} + \sigma_2\beta_2\pi_2\varphi\varepsilon\gamma_3 \\ \sigma_2(1-\beta_2)\gamma_{42} + \sigma_2\beta_2\pi_2\varphi\varepsilon\gamma_4 \end{pmatrix}$	$\begin{pmatrix} \sigma_3\beta_3\pi_3\varphi\nu \\ \sigma_3(1-\beta_3)\rho_{23} + \sigma_3\beta_3\pi_3\varphi\varepsilon(1-\gamma_3-\gamma_4) \\ \sigma_3(1-\beta_3)(1-\rho_{23}-\gamma_{43}) + \sigma_3\beta_3\pi_3\varphi\varepsilon\gamma_3 \\ \sigma_3(1-\beta_3)\gamma_{43} + \sigma_3\beta_3\pi_3\varphi\varepsilon\gamma_4 \end{pmatrix}$	$\begin{pmatrix} \sigma_4\beta_4\pi_4\varphi\nu \\ \sigma_4(1-\beta_4)\rho_{24} + \sigma_4\beta_4\pi_4\varphi\varepsilon(1-\gamma_3-\gamma_4) \\ \sigma_4(1-\beta_4)\rho_{34} + \sigma_4\beta_4\pi_4\varphi\varepsilon\gamma_3 \\ \sigma_4(1-\beta_4)(1-\rho_{24}-\rho_{34}) + \sigma_4\beta_4\pi_4\varphi\varepsilon\gamma_4 \end{pmatrix}$

Notes: The demographic model is a matrix model (Caswell 2001) based on vital rates (Jongejans et al. 2006, 2008). The matrices represent annual demographic transitions from the end of autumn of one year to the end of autumn a year later. The four stage classes are seeds in the seed bank (SB), small rosettes (S) that have <20% probability of surviving and flowering in the next year, medium-sized rosettes (M), and large rosettes (L) that have >80% chance of surviving and flowering next year. The dispersal model is the Wald analytical long-distance dispersal (WALD) model (Katul et al. 2005), which gives the distribution of dispersal distances, r , and is integrated over terminal velocity and seasonal wind conditions to give the seasonal dispersal kernel (using the approach of Skarpaas and Shea [2007]; see also Jongejans et al. [2008] for computational details). See Table 2 for parameter definitions.

TABLE 2. Demographic vital rate and dispersal parameter estimates for each of the three populations of the invasive thistle *Carduus nutans* (Jongejans et al. 2008) and their associated elasticity values for the population growth rate, λ , and the population spatial spread rate, c^* .

Parameter	Abbreviation	La Cavalerie, France (native range)	
		Vital rate	λ elasticity
Demographic parameters			
Survival of seed in SB	σ_1	0.2597	0.0724
Survival of S	σ_2	0.4831	0.5137
Survival of M	σ_3	0.8235	0.1321
Survival of L	σ_4	1.0000	0.1866
Growth of establishing seed to M	γ_3	0.0396	0.0110
Growth of establishing seed to L	γ_4	0.0099	0.0102
Growth of surviving, not-bolting S to M	γ_{32}	0.1256	0.0540
Growth of surviving, not-bolting S to L	γ_{42}	0.0205	0.0433
Retrogression of surviving, not-bolting M to S	ρ_{23}	0.0000	0.0000
Growth of surviving, not-bolting M to L	γ_{43}	0.0000	0.0000
Retrogression of surviving, not-bolting L to S	ρ_{24}	0.0000	0.0000
Retrogression of surviving, not-bolting L to M	ρ_{34}	0.0000	0.0000
Bolting of surviving S	β_2	0.0250	0.0016
Bolting of surviving M	β_3	0.9286	-0.0486
Bolting of surviving L	β_4	0.6000	-0.1234
Potential seed production by S	π_2	62	0.0144
Potential seed production by M	π_3	65	0.1192
Potential seed production by L	π_4	93	0.0626
Potential seed escaping from floral herbivory	φ	0.0925	0.1962
New seed entering SB	ν	0.3235	0.0953
New seed establishing seedling	ε	0.1148	0.1008
Seed from SB establishing seedling	ε_1	0.1148	0.0953
Dispersal parameters			
Geometric mean terminal seed settling velocity (m/s)	F	0.9840	...
Standard deviation of $\ln(F)$	σ_F	0.2055	...
Mean release height (mean plant height) (cm)	H	22	...
Vegetation height (cm)	h	4	...
Geometric mean wind speed at 10 m (m/s)	U	3.7371	...
Standard deviation of $\ln(U)$	σ_U	0.6458	...

Note: The stage classes in the matrix model were: seeds in the seed bank (SB), small (S), medium-sized (M), and large (L) rosettes. The stage class boundaries between the S and M stages and between the M and L stages were 26.3 cm² and 60.7 cm² for the French population, 20.8 cm² and 43.4 cm² for the Australian population, and 83.1 cm² and 175.0 cm² for the New Zealand population, respectively. Stochastic elasticity results are based on 10 000 runs of the simulation model. Ellipses represent quantities for which no parameters exist. There are no λ elasticity results for dispersal parameters, as dispersal does not affect local demography. There are no c^* elasticity values for the French population as there is no spread when $\lambda < 1$. Note that elasticities can be compared across sites, but that vital rate λ elasticities and c^* elasticities cannot be compared to one another as the raw elasticities do not sum to any particular value (unlike the element-based elasticities, which sum to 1 and to the reciprocal of the natural logarithm of the dominant eigenvalue of the combined demography-dispersal matrix [Neubert and Caswell 2000], respectively). Data sources are: for La Cavalerie, France, Sheppard et al. 1989, 1994, Jongejans et al. 2006, 2008; for Kybeyan, Australia, Shea et al. 2005, Jongejans et al. 2008; for Midland, New Zealand, Shea and Kelly 1998, Shea et al. 2005, Jongejans et al. 2008.

TABLE 1. Extended.

Dispersal model (WALD)	
$p(r) = \left(\frac{\xi'}{2\pi r^3}\right)^{\frac{1}{2}} \exp\left(-\frac{\xi'(r-\mu')^2}{2\mu'^2 r}\right)$	
where location parameter μ' and the scale parameter ξ' are given by	
$\mu' = \frac{HU}{F} \quad \text{and} \quad \xi' = \left(\frac{H}{\sigma}\right)^2$	

model equations are shown in Table 1, and dispersal parameter definitions and values are listed in Table 2.

In general, the vital rates and dispersal parameters differ quite strongly between populations (Table 2). For example, the terminal seed settling velocity, F , is much

lower in both invaded ranges (seeds fall less quickly and hence disperse further than in the native range), and the growth of small rosettes into the large class in the next year, γ_{42} , is much higher in the Australian population than in either of the other two locations. However, the relative importance of any differences (or lack thereof) can only be assessed once the elasticities are calculated.

The demographic and dispersal models for each of the three native or invaded-range locations are combined to allow the modeling of spatial spread using integrodifference equations (Neubert and Caswell 2000, Neubert and Parker 2004, Buckley et al. 2005, Jacquemyn et al. 2005, Lewis et al. 2006, Bullock et al. 2008, Jongejans et al. 2008). The models assume asymptotic growth rates within populations and that the environment is spatially homogeneous; obviously these are simplifications of the real world, but the models nonetheless allow us to

TABLE 2. Extended.

Abbreviation	Kybeyan, Australia (invaded range)			Midland, New Zealand (invaded range)		
	Vital rate	λ elasticity	c^* elasticity	Vital rate	λ elasticity	c^* elasticity
σ_1	0.4430	0.0557	0.2435	0.0382	0.0034	0.0026
σ_2	0.0167	0.0492	0.2405	0.1164	0.6711	0.6908
σ_3	0.0818	0.0352	0.1761	0.6813	0.0472	0.0413
σ_4	0.4393	0.7642	3.9045	0.7532	0.0424	0.0371
γ_3	0.0841	0.0296	0.1485	0.0000	0.0000	0.0000
γ_4	0.0999	0.6900	3.5436	0.0000	0.0000	0.0000
γ_{32}	0.1786	0.0006	0.0027	0.1065	0.0449	0.0393
γ_{42}	0.6786	0.0438	0.2130	0.0651	0.0405	0.0355
ρ_{23}	0.0000	0.0000	0.0000	0.3333	-0.0002	-0.0001
γ_{43}	0.8333	0.0149	0.0726	0.6667	0.0002	0.0001
ρ_{24}	0.1667	-0.0029	-0.0143	1.0000	-0.0002	-0.0001
ρ_{34}	0.3333	-0.0056	-0.0271	0.0000	0.0000	0.0000
β_2	0.1765	-0.0053	-0.0247	0.2620	0.5264	0.5646
β_3	0.5385	0.0005	0.0074	0.9516	0.0354	0.0327
β_4	0.9362	0.6189	3.2014	0.9828	0.0421	0.0368
π_2	125	0.0043	0.0222	2437	0.5643	0.5976
π_3	349	0.0192	0.0983	2776	0.0466	0.0408
π_4	1168	0.7549	3.8596	3576	0.0424	0.0371
ϕ	1.0000	0.7784	3.9800	1.0000	0.6533	0.6756
v	0.4300	0.0956	0.4540	0.1570	0.2359	0.2149
ε	0.0194	0.6828	3.5260	0.0194	0.4174	0.4607
ε_1	0.0048	0.0956	0.4540	0.1847	0.2359	0.2149
F	0.5716	...	-1.5320	0.4287	...	-1.0583
σ_F	0.1774	...	0.0818	0.1961	...	-0.1695
H	90	...	1.2555	57	...	1.0432
h	4	...	-0.1522	4	...	-0.3985
U	3.9570	...	1.4282	3.5365	...	1.2506
σ_U	0.6064	...	1.3364	0.7541	...	0.8670

TABLE 3. Management strategies and model manipulations and their effects on population growth rate, λ , and population spread rate, c^* , of the invasive thistle *Carduus nutans* in Australia and New Zealand.

Management strategy	Impact of management	Vital rate manipulations
No control†	none	none
Receptacle weevil <i>Rhinocyllus conicus</i>	reduces seed production by 30% of measured field values in Australia ^A reduces seed production by 35.7% of measured field values in New Zealand ^B	ϕ is multiplied by 0.7 ϕ is multiplied by 0.643
Receptacle gallfly <i>Urophora solstitialis</i>	reduces seed production by 70% of measured field values ^C	ϕ is multiplied by 0.3
Root-crown weevil <i>Trichosiromalus (mortadelo or horridus)</i>	reduces plant growth by 86.6% ^D and hence survivorship and fecundity are indirectly affected ^E	all 5 γ multiplied by 0.134 H multiplied by 0.815 for New Zealand population ^F ‡ H multiplied by 0.697 for Australian population ^G
Lethal herbicide	reduces the probability of rosette and seedling survival to 5% or 3% (depending on differences in application success) in that year ^H	all 4 σ multiplied by 0.05 or 0.03 (assuming size independent); as lethal, assume nothing dispersal-related is affected at 5% at 3%
Crash grazing	consists of 3–4 times the regular grazing pressure and leads to a 20% reduction in the probability of survivorship for rosettes and seedlings in that year ^I §	one season: all 4 σ multiplied by 0.8 two seasons: all 4 σ multiplied by 0.64
Spray-grazing	application of sublethal dose of herbicide (usually 0.5 to 0.1 the recommended rate) followed by very high stocking rates of sheep or cattle (7 or more DSE/ha) enclosed in the infested paddock ~1 week after herbicide application; reduces rosette and seedling survivorship to 1% ^J ¶	all 4 σ multiplied by 0.01¶

Notes: Shea et al. (2006) collated information on the large number of possible management strategies that have been used for this species, including empirical estimates of impact. The estimates and the modification of the vital rates in the matrix model are summarized here, including additional data on dispersal-related parameters. All c^* results are based on 10000 simulations. For the Australian population, because λ is <1 for all management scenarios, c^* does not exist, and there is no projected spread. See Table 2 for an explanation of parameter abbreviations. References are (by superscripted letter): (A) Sheppard et al. 1994, Kelly and McCallum 1995, Woodburn 1996b; (B) Kelly and McCallum 1990; (C) Sheppard et al. 1994, Woodburn 1996a, b; (D) Woodburn 2000; (E) Cartwright and Kok 1985, Woodburn 1997; (F) Groenteman 2007; (G) Woodburn 1997; (H) Popay et al. 1989, Dellow 1996, Harrington 1996; (I) Popay and Medd 1995, Huwer et al. 2005; (J) Pearce 1969, Huwer et al. 2005. The abbreviation DSE stands for “dry sheep equivalents.”

† For Australia, “no control” resulted in a c^* of 4.8994.

‡ Fitted mean height for plants not infested with *T. horridus* was 683 mm, so the 126 mm effect by moderate infestation was calculated to be 18.5%.

§ Might affect h (R. Huwer, *personal communication*), but no data exist; this possibility motivates the sensitivity analysis (Fig. 3).

¶ Might affect H and h , but no data exist; this possibility motivates these sensitivity analyses.

usefully compare different scenarios. As the joint model is stochastic, we repeated all simulations 10000 times (unless otherwise stated) and used the medians of these runs to exclude potential extreme outliers arising from the integrated WALD model. This joint model then allows us to project both population growth (λ) and population spread (c^*) rates for all locations. Standard sensitivity and elasticity analyses (Caswell 2001) can be performed on the model and examined at both the matrix element level (a relatively common approach; see Table 1) and at the vital rate level (a relatively new approach; see Table 2) of organization; we conducted both types of analysis here. Comparisons of elasticities for population growth and spread give insights into the

potential for different relative responses to changes in key vital rates or life cycle transitions.

As *C. nutans* is an important economic weed, a wide variety of single and integrated management strategies has been used to attempt to control it (Shea et al. 2006). Approaches include a wide range of levels and timing of conventional weed control, such as herbicide and grazing strategies (Popay and Medd 1995). Several insect biocontrol agents have been released in the invaded range; the three key agents are the receptacle weevil *Rhinocyllus conicus* Frölich, the receptacle gallfly *Urophora solstitialis* L., and the root-crown weevil *Trichosiromalus horridus* (Panzer) (Julien and Griffiths 1999). Note that *T. horridus* in Australia was recently

TABLE 3. Extended.

Australia		New Zealand			
λ	Reduction in λ (%)	λ	Reduction in λ (%)	c^*	Reduction in c^* (%)
1.203	---	2.684	---	21.2519	---
0.926	23.0	2.140	20.2	16.9081	20.4
0.875	27.3	2.032	24.3	15.7968	25.7
0.593	50.7	1.315	51.0	7.0769	66.7
0.496	58.8	2.467	8.1	19.7340	7.1
0.496	58.8	2.467	8.1	14.9409	29.7
0.496	58.8	2.467	8.1	12.0881	43.1
0.111	90.8	0.380	85.8	---	---
0.079	93.4	0.285	89.4	---	---
0.985	18.1	2.268	15.5	18.0113	15.2
0.809	32.8	1.926	28.2	15.0009	29.4
0.040	96.7	0.157	94.2	---	---

redescribed as *T. mortadelo* (Alonso-Zarazaga and Sánchez-Ruiz 2002), but that this is still under debate as the insects are very similar morphologically and ecologically and their distribution patterns are puzzling (Groenteman et al. 2008); where there is uncertainty we here refer to *Trichosiocalus*. Many of these management methods have been combined in the field, with varying degrees of success (Moore et al. 1989, Popay and Medd 1995, Huwer et al. 2005). Table 3 shows a summary of these management strategies, their estimated impacts (from observational or experimental studies listed in the table), and the associated vital rate modifications made to the models. For example, since *U. solstitialis* affects developing inflorescences, we simulated its effects by lowering ϕ , the probability that seeds escape floral herbivory, by 70%. In this manner, we assessed all listed management strategies for their impacts on population growth and spread in both invaded-range scenarios.

Finally, in order to assess broad patterns in the effects of key vital rate group changes on growth and spread rates, we systematically varied survival parameters, σ ; growth parameters, γ ; seed escape from floral herbivory, ϕ ; seedling establishment parameters, ϵ ; mean plant height, H ; and vegetation height, h , over appropriate ranges to assess their potential impact in both Australia

and New Zealand. In this analysis, 1000 iterations were run to generate each point on the graph. This approach may also potentially suggest vital rates that have been overlooked as promising management targets.

RESULTS

The main projected population growth results for the native and two invaded-range populations are known from previous work (Shea et al. 2005, Jongejans et al. 2008). The population growth rates in both the Australian and New Zealand populations are greater than 1 (indicating sustained population growth). The projected population growth rate in New Zealand ($\lambda = 2.7$) is more than twice that in Australia ($\lambda = 1.2$), while the spread rate in New Zealand ($c^* = 21.3$ m/yr) is more than four times that in Australia ($c^* = 4.9$ m/yr). Note that the native range population growth rate is less than 1 ($\lambda = 0.6$), so there is no spread. Note also that these c^* estimates (and c^* estimates for additional populations in Kansas, USA, $c^* = 5.6$ m/yr; Pennsylvania, USA, $c^* = 82$ m/yr; and France, $c^* = 0.34$ m/yr with $\phi = 1$) differ from those presented in Jongejans et al. (2008). This is because the site-specific wind speeds (used to calculate wind dispersal at plant height H while assuming a wind speed profile) were measured at 10 m, but the earlier model erroneously assumed 2 m.

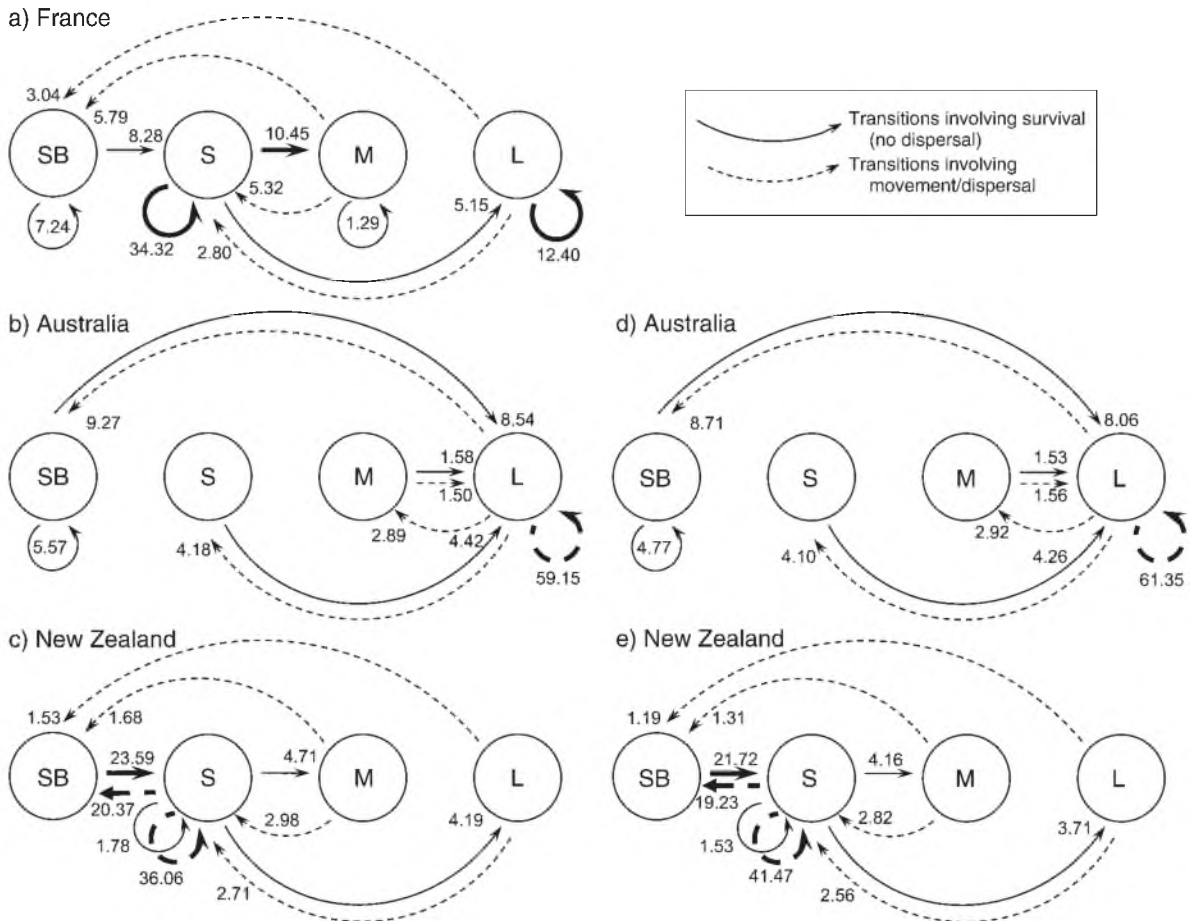


FIG. 1. Life cycle representation of elasticities of population growth, λ , and population spread, c^* of the invasive thistle *Carduus nutans*. (a–c) Transition-based λ elasticities for France (native range, $\lambda = 0.602$), Australia (invaded range, $\lambda = 1.203$), and New Zealand (invaded range, $\lambda = 2.684$), respectively; (d, e) c^* elasticities for Australia ($c^* = 4.8994$) and New Zealand ($c^* = 21.2519$), respectively. Note that there are no values of c^* elasticities for France; there is no spread when a population is in decline ($\lambda < 1$). The four stage classes are seeds in the seed bank (SB), small rosettes (S) that have <20% probability of surviving and flowering in the next year, medium-sized rosettes (M), and large rosettes (L) that have >80% chance of surviving and flowering next year. The λ elasticities are presented as percentages (they sum to 100%). However, c^* elasticities of matrix elements do not necessarily add up to 1. Here we show percentage data (c^* elasticities divided by the sum of the elasticities [which is 0.8458 for New Zealand and 4.0763 for Australia] and multiplied by 100 to give a percentage) in order to facilitate comparison between invaded ranges and with the λ elasticities (Neubert and Caswell 2000). In all panels, solid lines represent transitions involving stasis (no movement), while broken lines represent transitions that do involve dispersal. Only transitions with scaled elasticities >1% are shown; thick lines represent elasticities >10%.

Clearly, these differences in λ and c^* arise from differences in the life cycle of the species in the different locations. Examination of the underlying vital rates (Table 2) gives some idea of pairwise differences, but elasticity analyses for vital rates (Table 2) and stage transitions (Fig. 1) give deeper insights: larger elasticity values imply that any perturbation to that vital rate will have larger impacts on the growth or spread rate; smaller values imply smaller impacts. Negative elasticity values imply that an increase in that parameter will have a negative effect on population growth or spread. Negative elasticities are seen for retrogression vital rates (if plants die back then that reduces population growth and spread) and for terminal velocities (if seeds have

higher terminal velocities they fall to the ground more quickly and hence do not disperse as far, reducing spread) and vegetation height (the higher the surrounding vegetation, the shorter the distance that seeds can fall before they are intercepted and their dispersal is curtailed). Additionally, the elasticity values of the French bolting probabilities (bolting is the development of flowering stalks and is an irreversible commitment to flowering and subsequent death in these monocarpic plants) are negative; this is because in this declining population, survival is more important for population size than sexual reproduction. Interestingly, there is also a negative elasticity for the probability of bolting of small plants in the Australian population. This latter can

be better understood once the transition element elasticities are studied in more detail (Fig. 1).

Fig. 1 shows the stage-transition-based elasticities of both λ and c^* ; it examines the importance of perturbation in transitions between the seed bank (SB) and small (S), medium (M), and large (L) rosette categories to population growth (Fig. 1a–c) and spread (Fig. 1d, e). The French population growth is driven most strongly by the S–S, the S–M, and the L–L transitions. In the Australian population the L–L elasticity dominates, which explains why bolting of small plants, as shown in the vital rate elasticity results, negatively impacts population growth; bolting of small rosettes trades off with the more important transition (i.e., with higher elasticity values) of small rosettes that survive and grow to become large. Note that the elasticity life cycle diagram for Australia differs significantly from the elasticity results presented in Shea et al. (2005), despite being modeled using the same data. There are four main reasons for these differences (see also Jongejans et al. 2008). First, there was an error in the 2005 paper in how the raw data were averaged to generate matrix elements; this artificially inflated some survival and growth rates, and we take this opportunity to correct that error in print. Second, to ensure structural similarity of the model for all three locations, we now calculate the probability of flowering directly from the raw data (not by fitting and using a function, as previously). Third, we no longer assume that all seedlings grow only into small rosettes. Additionally, there is a fourth possible reason for differences; the shift from a matrix-element-based approach to a vital-rate approach (Jongejans et al. 2008) may have made a minor quantitative difference in both populations. These four differences cause significant changes to the elasticity results. The implication is that Australian population growth is more due to large plants producing offspring that also grow to a large size than due to survival of rosettes, as previously thought (Shea et al. 2005). Fortunately, the Australian management implications of the earlier work are still largely supported (see *Management results*, below). In the New Zealand population, the largest λ elasticities are for the S–S, SB–S, and S–SB transitions. This does largely agree with Shea et al. (2005); here the only difference is in the way the probability of flowering was calculated (from the raw data, rather than fitting a function), which leads to minor quantitative differences only.

A comparison between the French and New Zealand λ elasticities illustrates the utility of the vital rate approach over the simpler transition-based-only approach used previously (Shea and Kelly 1998, Shea et al. 2005). In both populations, the largest elasticity is for the S–S transition, contributing an average of 36% (34.3% in France, 37.8% in New Zealand). For many purposes, this information would suffice. However, in the context of tailoring management strategies to target population growth or spread, or for predicting spread rates, there is an obvious critical difference; the French

S–S elasticity pertains entirely to stasis, while the New Zealand S–S elasticity has only a minor stasis component and is dominated by reproduction and dispersal. In other words the important French S–S transition concerns small rosettes that survive as small plants to the next year, while the New Zealand S–S transition concerns small plants that flower to produce new small plants in the following year. If only general demographic effects are of interest, the distinction is unimportant. However, if the focus is on management or on spatial spread vs. local growth issues, the distinction may be very important. For example, if *all* of the New Zealand S–S transition was attributable to dispersal, then the spread rate does not change significantly (most of the element is already dispersal). However, if it was all attributable to stasis, then the spread rate would decrease 11.5% from $c^* = 21.3$ m/yr to $c^* = 18.8$ m/yr (while λ remains unchanged). Failing to distinguish the two makes no difference to estimated demographic rates at the matrix element level, but could lead to significant errors in estimations of spread rate and management impact.

Fig. 1d, e also show the stage transition-based elasticities for c^* . The largest elasticities for c^* are the same as the largest elasticities for λ . Broadly, this implies that for a particular part of the invaded range, spread and population growth are both affected by the same key transitions in the life cycle of the plant.

However, closer examination shows that there are subtle qualifiers to this conclusion. Fig. 2 shows the transition-element-based λ elasticities correlated against the c^* elasticities for Australia and New Zealand. Most points lie along the line, and the vital-rate-based elasticities (Table 2) are also fairly linear (not shown). This implies that those elements (or vital rates) are equally important for population growth as for spread. However, some points do not lie along the line. Points that lie above the line have a relatively higher elasticity value for wave speed, c^* , while points that lie below the line have a relatively higher elasticity value for population growth rate, λ . For Australia, the one point above the line relates to the L–L transition (involving dispersal, not survival). Even though it is the largest elasticity for both λ and c^* , its relative importance to spread is higher. Similarly, the New Zealand S–S elasticity (again through dispersal) is considerably higher than expected from the local population dynamics.

Two transitions have values that were lower than expected in New Zealand: establishment of small plants from the seed bank (SB–S) and contributions from small plants to the seed bank (S–SB). These transitions are always part of life cycle loops (van Groenendael et al. 1994) that do not involve dispersal in at least one step. Thus, establishment from the seed bank (e.g., SB–S) is very important locally, but less important for spread because there is no dispersal involved. Similarly, the S–SB step does involve dispersal, but slows the spread as

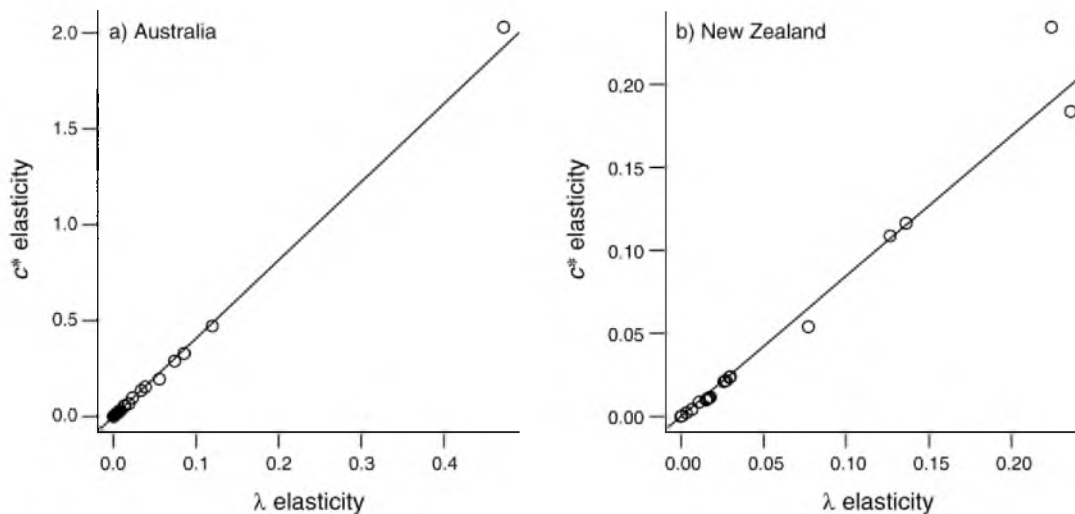


FIG. 2. Elasticity values of the matrix elements (based on a 7×7 matrix; Jongejans et al. 2008) for population growth, λ , vs. spread, c^* of the invasive thistle *Carduus nutans*. The results are based on 10 000 simulations. The elasticities are the unscaled values (Fig. 1 shows the scaled results), but the line in each panel is scaled (based on the sum of the c^* elasticities, which scale to the reciprocal of the natural logarithm of the dominant eigenvalue of the combined demography–dispersal matrix; Neubert and Caswell 2000: Eq. 27). For Australia the sum of the c^* elasticities is 4.0763; for New Zealand the sum is 0.8458. Most elasticities lie along the line, implying that perturbations in those transitions are equally important to local population growth and to spread. Points above the line represent transitions that, if perturbed, would cause greater changes in spread than in demography; points below the line imply the opposite.

seeds go into the seed bank for at least a year. Most of these slightly anomalous transitions highlighted by Fig. 2 thus imply that specific targeting of these transitions might disproportionately benefit management aimed at either reducing spread (L–L in Australia, S–S in New Zealand) or reducing population growth (SB–S and to a lesser extent S–SB in New Zealand).

Management results

To explicitly explore the relative impacts of different management strategies on population growth vs. spread, we modeled the documented impacts of a wide range of weed management strategies on λ and c^* for both of the invaded-range populations (Table 3). Most of these impacts can also be seen in Fig. 3. As expected, all management strategies reduce both population growth and spread below the no-control baseline values.

For the three biological control agents, *Trichosirocalus* is projected to have the largest effect on growth rates in Australia, followed closely by *U. solstitialis* and then *R. conicus* (Table 3). In New Zealand, however, *U. solstitialis* is projected to most reduce population growth, then *R. conicus* and finally *T. horridus*. Of the single management options, lethal herbicide generated the most drastic reductions in population growth in both countries (85–94%; Table 3). Only the integrated spray–grazing approach (a combination of sublethal herbicide and high stocking rates) generated larger population growth reductions (94–97%). Crash-grazing (3–4 times the normal grazing pressure) performed less well (Table 3), but improved when applied in more than one season (see also Shea et al. 2006 for Australia).

In the Australian scenario, all management approaches tested reduced λ below 1; in such situations there is no spatial spread (assuming spatial homogeneity). In the New Zealand scenario, this also occurred for the most extreme management strategies (spray–grazing and lethal herbicide; Table 3). Crash-grazing in New Zealand (based on impact data from Australia) leads to very similar reductions in both population growth rates, λ , and spread rate, c^* (~15% if applied in one season, ~28–29% if applied in two). This similarity in the impact on λ and c^* is also seen for the impact of *R. conicus*, assuming either Australian or New Zealand attack rates (Table 3). However, as previously predicted (Shea 2004) optimal management to control population growth may not always have similar effects on population spread. Effects are highly correlated (Figs. 1 and 2; data points in Fig. 2 mainly lie along the line), and obviously if $\lambda < 1$, then c^* does not exist, and there is no projected spread, but there is some scope for important differences (see the outliers in Fig. 2). The relative effect of *U. solstitialis* (51.0% reduction in λ , 66.7% reduction in c^*) differed rather more dramatically than that for *R. conicus*. For *T. horridus*, if we include only documented effects on rosette growth, then λ and c^* results are similar (~7–8%). Although there is probably a positive relationship between rosette size and ultimate flowering plant height, there is no published information on this, so it has not explicitly been included in this (or previous) models. Thus, our spread models all assume the average documented plant height in each population. However, there are data on *Trichosirocalus*-induced height reductions for both

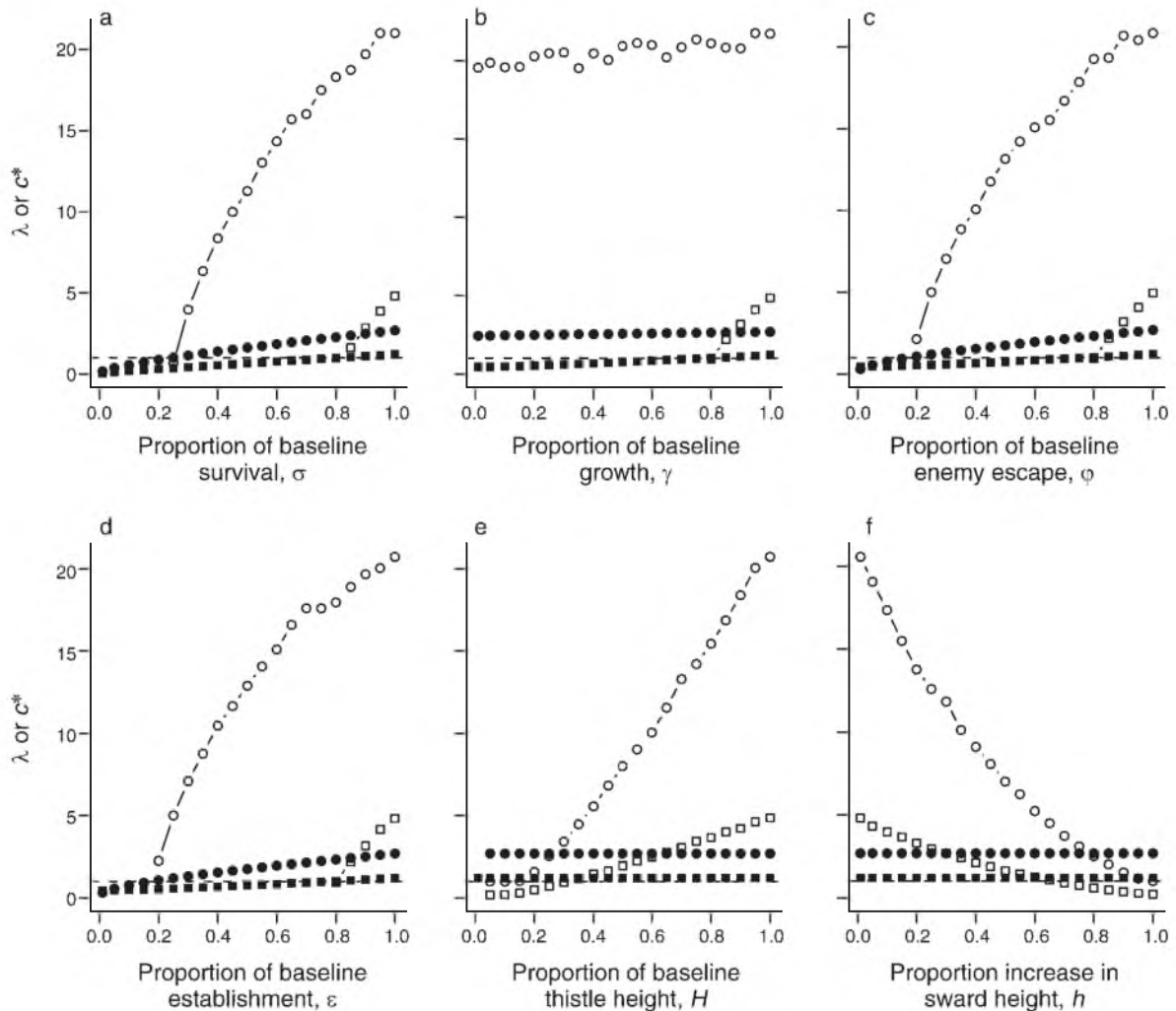


FIG. 3. Effect of systematic proportional decreases in all σ , all γ , ϕ , both ϵ , as well as decreases in H (down to baseline h ; $h = 0.04$ m for both invaded ranges) and increases in h (up to H ; $H = 0.9$ m for Australia and $H = 0.57$ m for New Zealand) for λ (solid symbols) and c^* (open symbols) of the invasive thistle *Carduus nutans* for both Australia (squares) and New Zealand (circles). Each point is the outcome of 1000 runs of the stochastic simulation. The horizontal dotted line is the $\lambda = 1$ line; if $\lambda < 1$, then c^* does not exist. See Table 2 for explanations of parameter abbreviations.

Australia and New Zealand. In the New Zealand scenario, this reduces c^* by nearly 30% (while λ reductions remain at $\sim 8\%$). As $\lambda < 1$ in Australia, height effects cannot be assessed there directly; however, if observed Australian height reductions are applied in New Zealand, a 43% reduction in c^* results (again with only an 8% reduction in λ). *Urophora solstitialis* has the largest impact on both λ and c^* in New Zealand, so management recommendations would not change, but note that *R. conicus* in New Zealand is ranked above *T. horridus* from the point of view of impacts on λ , but that this is not true from the point of view of c^* . With the caveats that biological control is actually very spatially and temporally variable and that the insect dynamics may themselves show context dependency, our model implies that in this case the better of the two agents to

control spread is not the better agent if control of population growth is the objective.

Systematic modification of key vital rates allows us to explore their potential impact on spread and population growth rates (Fig. 3). This also may potentially suggest vital rates that have not previously been the target of management, yet which might generate strong outcomes. The results for decreases in survival (σ ; Fig. 3a), escape from insect floral herbivory (ϕ ; Fig. 3c), and establishment (ϵ ; Fig. 3d) are all similar for both population growth and spread. In all three cases decreases in these parameters result in a slow decrease in λ and a more dramatic decrease in c^* . To stop the Australian and New Zealand populations from spreading, 20% and 80% reductions would be required, respectively. In the case of survival and establishment (Fig. 3a, d) this highlights a strong potential for

management strategies that specifically target seedling establishment and survival. Certainly, maintenance of a sward of dense vegetation has been documented to be an effective tool for controlling early life stages (Phung and Popay 1981, Kelly and McCallum 1990, Rauschert 2006), and the effect of such management on spread would be significant, but this can be financially costly in heavily grazed areas or difficult in areas, such as Australia, where drought often limits vegetation growth. The impact of grazing and sward management would also likely be mediated through dispersal parameters. Lowering seed release height (i.e., plant height) down to sward height (Fig. 3e) or alternatively increasing sward height to seed release height in the models (Fig. 3f) does not affect local population growth but does significantly reduce spread rates of both populations. This indicates that these dispersal-related parameters are efficient targets as well, but only for the case of spread management. As to be expected from the differences in the importance of small vs. large rosettes between Australia and New Zealand, reducing growth rates only has a major impact in Australia; there is little sensitivity to changes in these parameters in New Zealand (Fig. 3b).

DISCUSSION

In this paper, we have assessed the relative contributions of changes in vital rates to both population growth, λ , and population spread, c^* . In doing so, we have illustrated the benefits to be gained from a vital rate approach to modeling populations. We have also confirmed previous predictions (Shea 2004) that optimal management may strongly depend on the detailed objective (particularly extending the objective of “control” to more specifically stating “reducing abundance” or “limiting spread”), confirmed old and presented new management results, and also suggested underutilized management strategies for future exploration.

As previously reported, and as expected, this species has higher growth and spread rates in the invaded range (represented by the Australian and New Zealand populations in this study) than in the native range (represented by the French population). Both are higher in New Zealand than in Australia, but not by the same proportion: λ in New Zealand is more than twice as high, while c^* is more than four times as high as in Australia. Spread rate differences arise from both demography and dispersal (the details can be found in a Life Table Response Experiment analysis in Jongejans et al. [2008: Appendix S2]), while λ depends only on demography. The relative difference between these c^* and λ differences result from interactive effects of changed demography and dispersal. This relative difference already suggests that management impacts and ranking may differ both between the invaded ranges (Shea et al. 2005) and for different objectives.

For the three biological control agents, *Trichosirocalus* is projected to have the largest effect on growth rates in

Australia, followed closely by *U. solstitialis* and then *R. conicus* (Table 3). This agrees qualitatively with prior results based on a matrix element approach presented in Shea et al. (2005; the small quantitative differences arise from the differences in parameterization described in *Results* and the change from an element-based to a vital-rate-based approach) and with prior results based on an individual-based modeling (IBM) approach in Shea et al. (2006) (the ranking is identical for all management strategies tested here; quantitative comparisons are not possible as the IBM measured success based on the cumulative probability of extinction over multiple stochastically simulated populations). In New Zealand, *U. solstitialis* is projected to most reduce population growth, then *R. conicus*, and finally *T. horridus*. The optimal strategy is unchanged from prior work (*U. solstitialis* is the best agent), but the relative ranking of the other two lesser agents has now changed; previously *T. horridus* was ranked second. This shift in ranking is mainly attributable to *T. horridus*; in the previous study it was projected to nearly halve the population growth rate, whereas the present paper suggests an expected 8% decline in λ . This is a direct consequence of the change from an element-based to a vital-rate-based approach. *Trichosirocalus horridus* was previously modeled as having an effect on the whole of each element it affected, but the vital-rate approach allows us to explicitly separate survival and reproductive terms. As *T. horridus* affects γ parameters (growth of nonflowering, surviving plants), and as the major part of the affected transitions at the New Zealand site, such as S–S, are reproductive, this means *T. horridus* now has a much smaller impact than previously modeled.

In most respects there is a strong congruence for elasticities of population growth, λ , and spread, c^* , in a given part of the invaded range (Fig. 1). This agrees with earlier work in other systems (e.g., Caswell et al. 2003), which found that spread and growth at a location are both most strongly affected by the same life cycle transitions. However, departures from the scaled 1:1 relationship (Fig. 2) indicate vital rates that may disproportionately affect either spread or growth. For example, the L–L transition in Australia has very large transition-based elasticity values, both for λ and for c^* (Fig. 1). However, as this transition is dominated by reproduction of large plants (rather than survival to the next year) it is relatively more important to c^* than to λ (Fig. 2a). Similarly, as the New Zealand S–S transition is predominantly dispersal-related, it lies well above the scaled 1:1 line, while the SB–S and S–SB transitions are relatively more important to population growth, as explained in *Results*.

The New Zealand S–S transition illustrates that considerable insight can be gained from a vital rate approach over an element-based matrix model. Element-based comparisons for France and New Zealand would note the similarity of this term in each location, whereas the vital-rate-based approach strongly demonstrates

how different they are and how critical the distinction is if understanding spread is an objective (see *Results*). This same transition also illustrates that management projections may improve in specificity as a result of the greater detail included. The same management strategy, with impact described in the same way, may need to be incorporated in different model versions in different ways. In this paper, we have contrasted transition-based and vital-rate-based matrix approaches. They are very closely related. For example, in both cases, plant growth is modeled as the probability of moving between size classes (γ). In other models for this system, such as the IBM developed for Australian management (Shea et al. 2006) or in an integral projection model (IPM) structure (Metcalfe et al. 2008, 2009; E. Jongejans et al., *unpublished manuscript*) the actual size of individuals or their continuous size distribution is modeled, so that plant growth can be incorporated in more detail. However, despite strong structural similarities between the element and vital-rate-matrix approaches there are important differences. In the element-based approach, whole elements are perforce affected at the same time, even if some part of that element might not have been involved biologically. In the vital-rate-based approach alterations can be applied with finer resolution. As outlined above, the shift in relative ranking of *T. horridus* from second to third in projected impact in New Zealand is attributable to the change from an element-based matrix model, where the weevil affects an entire element (Shea and Kelly 1998, Shea et al. 2005), to a vital rate matrix model (as illustrated in this paper), which correctly delimits the role of plant growth in that element and hence reduces the projected impact of this weevil.

Finally, there is another advantage of the vital-rate approach: looking for management strategies that have not been considered previously or that might be more efficacious than previously considered. We modified key groups of vital rates to explore their impacts on λ and c^* . Establishment of fresh and older seed (ε , ε_1) is not directly impacted by any of the management strategies we explored, yet reducing establishment potentially has as strong an impact as reducing survival or increasing floral herbivory (Fig. 3). One possibility is to reduce overgrazing, reducing microsites for germination and establishment, as microsite availability has been found in field experiments to be key to thistle spread (Jongejans et al. 2007). This has been suggested before (Wardle et al. 1995, Rauschert 2006); our study suggests that further investigation might yield significant rewards. Lower stocking rates would likely also increase sward height, h , augmenting the reduction in dispersal and hence spread. The model also prompts us to look for other possible effects of existing management if spread reduction is important. Management impacts on dispersal parameters have been relatively little explored, though work is ongoing to assess insect impacts on dispersal parameters such as terminal velocity (K. M.

Marchetto et al., *unpublished manuscript*) and mowing impacts on demography and dispersal parameters such as seed production and plant height (R. Zhang and K. Shea, *unpublished manuscript*).

In large part other management results for population growth control broadly agreed with and confirmed earlier results. For the Australian population, as all tested management strategies reduced λ below 1, there are no spread predictions to rank. This mirrors the situation for the unmanaged (and managed) population projections in France. However, even though these local populations are not growing and spreading, dispersal is probably not unimportant: despite $\lambda < 1$ due to high levels of herbivory (Jongejans et al. 2006), the species has persisted in Europe for a long time, probably as a fugitive species in a metapopulation context. In New Zealand, a few of the higher impact management strategies also reduced λ below 1, and the relative reductions in λ and c^* were similar for other management strategies (e.g., crash-grazing). However, there were some strong differences in relative reductions in λ and c^* for *U. solstitialis* and also for *T. horridus* if plant height effects were taken into account. This changes the relative ranking of *R. conicus* and *T. horridus*, depending on whether control of population growth or population spread is the more desired outcome, and therefore could alter which of the two biocontrol agents was preferred for release in a new area. The possibility of such shifts in relative projected ranking have been predicted theoretically (Shea 2004), but never before demonstrated using field data.

ACKNOWLEDGMENTS

We thank Ronny Groenteman, Ruth Huwer, and Tim Woodburn for valuable information, discussions, and comments. This research was partly funded by the National Science Foundation (grants DEB-0315860 and DEB-0614065) and USDA-CSREES (Biology of Weedy and Invasive Plants) NRI grant 2002-35320-12289 to K. Shea. E. Jongejans acknowledges NWO-veni grant 863.08.006. The field work in New Zealand was in part funded by Landcare Research under the Outsmarting Weeds programme, FRST contract C10X0318.

LITERATURE CITED

- Allen, M., and K. Shea. 2006. Spatial segregation of congeneric invaders in Pennsylvania, USA. *Biological Invasions* 8:509–521.
- Alonso-Zarazaga, M. A., and M. Sánchez-Ruiz. 2002. Revision of the *Trichostirocalus horridus* (Panzer) species complex, with description of two new species infesting thistles (Coleoptera: Curculionidae, Ceutorhynchinae). *Australian Journal of Entomology* 41:199–208.
- Bogich, T., and K. Shea. 2008. A state-dependent model for the optimal management of an invasive metapopulation. *Ecological Applications* 18:748–761.
- Buckley, Y. M., E. Brockerhoff, L. Langer, N. Ledgard, H. North, and M. Rees. 2005. Slowing down a pine invasion despite uncertainty in demography and dispersal. *Journal of Applied Ecology* 42:1020–1030.
- Bullock, J. M., R. F. Pywell, and S. J. Coulson-Phillips. 2008. Managing plant population spread: prediction and analysis using a simple model. *Ecological Applications* 18:945–953.
- Cartwright, B., and L. T. Kok. 1985. Growth-responses of musk and plumeless thistles (*Carduus nutans* and *Carduus*

- acanthoides*) to damage by *Trichosirocalus horridus* (Coleoptera, Curculionidae). *Weed Science* 33:57–62.
- Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. Second edition. Sinauer, Sunderland, Massachusetts, USA.
- Caswell, H., R. Lensink, and M. G. Neubert. 2003. Demography and dispersal: life table response experiments for invasion speed. *Ecology* 84:1968–1978.
- Crawley, M. 1989. Insect herbivores and plant population dynamics. *Annual Review of Entomology* 34:531–564.
- de Kroon, H., J. M. van Groenendael, and J. Ehrlén. 2000. Elasticities: a review of methods and model limitations. *Ecology* 81:607–618.
- Dellow, J. J. 1996. Herbicide techniques for thistle management. *Plant Protection Quarterly* 11:276–277.
- Desrochers, A. M., J. F. Bain, and S. I. Warwick. 1988. The biology of Canadian weeds. 89. *Carduus nutans* L. and *Carduus acanthoides* L. *Canadian Journal of Plant Science* 68:1053–1068.
- DeWalt, S. J. 2006. Population dynamics and potential for biological control of an exotic invasive shrub in Hawaiian rainforests. *Biological Invasions* 8:1145–1158.
- Emery, S. M., and K. L. Gross. 2005. Effects of timing of prescribed fire on the demography of an invasive plant, spotted knapweed *Centaurea maculosa*. *Journal of Applied Ecology* 42:60–69.
- Groenteman, R. 2007. Multi-species interactions in weed biocontrol: *Carduus nutans* as a case study. Thesis. University of Canterbury, Christchurch, New Zealand.
- Groenteman, R., D. Kelly, S. V. Fowler, and G. W. Bourdot. 2008. Which species of the thistle biocontrol agent *Trichosirocalus* are present in New Zealand? Pages 145–149 in M. H. Julien, et al., editors. Proceedings of the 12th International Symposium on Biological Control of Weeds. CABI International, Wallingford, UK.
- Hansen, M. J., and S. D. Wilson. 2006. Is management of an invasive grass *Agropyron cristatum* contingent on environmental variation? *Journal of Applied Ecology* 43:269–280.
- Harper, J. L. 1977. Population biology of plants. Academic Press, London, UK.
- Harrington, K. C. 1996. Herbicide management and thistle control: how to avoid resistance. *Plant Protection Quarterly* 11:273–275.
- Huwer, R. K., D. T. Briese, P. M. Dowling, D. R. Kemp, W. M. Lonsdale, D. L. Michalk, M. J. Neave, A. W. Sheppard, and T. L. Woodburn. 2005. Can an integrated management approach provide a basis for long-term prevention of weed dominance in Australian pasture systems? *Weed Research* 45:175–192.
- Jacquemyn, H., R. Brys, and M. G. Neubert. 2005. Fire increases invasive spread of *Molinia caerulea* mainly through changes in demographic parameters. *Ecological Applications* 15:2097–2108.
- Jongejans, E., K. Shea, O. Skarpaas, D. Kelly, A. W. Sheppard, and T. L. Woodburn. 2008. Dispersal and demography contributions to population spread of *Carduus nutans* in its native and invaded ranges. *Journal of Ecology* 96:687–697.
- Jongejans, E., A. W. Sheppard, and K. Shea. 2006. What controls the population dynamics of the invasive thistle *Carduus nutans* in its native range? *Journal of Applied Ecology* 43:877–886.
- Jongejans, E., O. Skarpaas, P. W. Tipping, and K. Shea. 2007. Establishment and spread of founding populations of an invasive thistle: the role of competition and seed limitation. *Biological Invasions* 9:317–325.
- Julien, M. H., and M. W. Griffiths. 1999. Biological control of weeds: a world catalogue of agents and their target weeds. Fourth edition. CABI International, Wallingford, UK.
- Katul, G. G., A. Porporato, R. Nathan, M. Siqueira, M. B. Soons, D. Poggi, H. S. Horn, and S. A. Levin. 2005. Mechanistic analytical models for long-distance seed dispersal by wind. *American Naturalist* 166:368–381.
- Kelly, D., and K. McCallum. 1990. Demography, seed biology and biological control of *Carduus nutans* in New Zealand. Pages 72–79 in J. P. Palmer, editor. The biology and control of invasive plants. British Ecological Society, Cardiff, UK.
- Kelly, D., and K. McCallum. 1995. Evaluating the impact of *Rhinocyllus conicus* on *Carduus nutans*. Pages 205–211 in E. S. Delfosse and R. R. Scott, editors. New Zealand Proceedings of the 8th International Symposium on Biological Control of Weeds. Commonwealth Scientific and Industrial Research Organisation (CSIRO)/Lincoln University, Canterbury, New Zealand.
- Lewis, M. A., M. G. Neubert, H. Caswell, J. S. Clark, and K. Shea. 2006. A guide to calculating discrete-time invasion rates from data. Pages 169–192 in M. W. Cadotte, S. M. McMahon, and T. Fukami, editors. Conceptual ecology and invasion biology: reciprocal approaches to nature. Springer, Dordrecht, The Netherlands.
- McEvoy, P. B., and E. M. Coombs. 1999. Biological control of plant invaders: regional patterns, field experiments, and structured population models. *Ecological Applications* 9:387–401.
- Mertens, S. K., F. van den Bosch, and J. A. P. Heesterbeek. 2002. Weed populations and crop rotations: exploring dynamics of a structured periodic system. *Ecological Applications* 12:1125–1141.
- Metcalfe, C. J. E., M. Rees, Y. M. Buckley, and A. W. Sheppard. 2009. Seed predators and the evolutionarily stable flowering strategy in the invasive plant, *Carduus nutans*. *Evolutionary Ecology* 23:893–906.
- Metcalfe, C. J. E., K. E. Rose, D. Z. Childs, A. W. Sheppard, P. J. Grubb, and M. Rees. 2008. Evolution of flowering decisions in a stochastic, density-dependent environment. *Proceedings of the National Academy of Sciences (USA)* 105:10466–10470.
- Moore, W. B., C. J. Doyle, and A. Rahman. 1989. Economics of controlling *Carduus nutans* on grazed pasture in New Zealand. *Crop Protection* 8:16–24.
- Moran, V. C., J. H. Hoffmann, and T. Olckers. 2004. Politics and ecology in the management of alien invasive woody trees: the pivotal role of biological control agents that diminish seed production. Pages 434–439 in J. M. Cullen, D. T. Briese, D. J. Kriticos, W. M. Lonsdale, L. Morin, and J. K. Scott, editors. Proceedings of the XI International Symposium on Biological Control of Weeds. Commonwealth Scientific and Industrial Research Organisation (CSIRO), Entomology, Canberra, ACT, Australia.
- Neubert, M. G., and H. Caswell. 2000. Demography and dispersal: calculation and sensitivity analysis of invasion speed for structured populations. *Ecology* 81:1613–1628.
- Neubert, M. G., and I. M. Parker. 2004. Projecting rates of spread for invasive species. *Risk Analysis* 24:817–831.
- Pauchard, A., and K. Shea. 2006. Integrating the study of non-native plant invasions across spatial scales. *Biological Invasions* 8:399–413.
- Paynter, Q., S. V. Fowler, H. L. Hinz, J. Memmot, R. Shaw, A. W. Sheppard, and P. Syrett. 1996. Are seed-feeding insects of use for the biological control of broom? Pages 495–501 in V. C. Moran and J. H. Hoffman, editors. Proceedings of the IX International Symposium on Biological Control of Weeds. University of Capetown, Cape Town, South Africa.
- Pearce, G. A. 1969. Weed control in pastures: a practical approach for sheep areas. *Journal of the Department of Agriculture of Western Australia* 11:139–142.
- Phung, H. T., and A. I. Popay. 1981. Effect of pasture cover on the germination of certain weed seeds. *New Zealand Weed and Pest Control Conference Proceedings* 34:111–113.
- Popay, A. I., J. H. Butler, and F. A. Meeklah. 1989. Chemical control of nodding thistle (*Carduus nutans* L.) in New Zealand pastures. *Weed Research* 29:21–28.

- Popay, A. I., and R. W. Medd. 1995. *Carduus nutans* L. ssp. *nutans*. Pages 29–50 in R. H. Groves, R. C. H. Shepherd, and R. G. Richardson, editors. The biology of Australian weeds. Richardson, Melbourne, Victoria, Australia.
- Rauschert, E. S. J. 2006. Competitive interactions and associations of the invasive thistles *Carduus nutans* and *C. acanthoides*. Dissertation. The Pennsylvania State University, University Park, Pennsylvania, USA.
- Shea, K. 2004. Models for improving the targeting and implementation of biological control of weeds. *Weed Technology* 18:1578–1581.
- Shea, K., P. Amarasekare, P. Kareiva, M. Mangel, J. Moore, W. W. Murdoch, E. Noonburg, A. M. Parma, M. A. Pascual, H. P. Possingham, C. Wilcox, and D. Yu. 1998. Management of populations in conservation, harvesting and control. *Trends in Ecology and Evolution* 13:371–375.
- Shea, K., and D. Kelly. 1998. Estimating biocontrol agent impact with matrix models: *Carduus nutans* in New Zealand. *Ecological Applications* 8:824–832.
- Shea, K., D. Kelly, A. W. Sheppard, and T. L. Woodburn. 2005. Context-dependent biological control of an invasive thistle. *Ecology* 86:3174–3181.
- Shea, K., A. Sheppard, and T. Woodburn. 2006. Seasonal life-history models for the integrated management of the invasive weed nodding thistle *Carduus nutans* in Australia. *Journal of Applied Ecology* 43:517–526.
- Sheppard, A. W., J. M. Cullen, and J. P. Aeschlimann. 1994. Predispersal seed predation on *Carduus nutans* (Asteraceae) in southern Europe. *Acta Oecologica* 15:529–541.
- Sheppard, A. W., J. M. Cullen, J. P. Aeschlimann, J. L. Sagliocco, and J. Vitou. 1989. The importance of insect herbivores relative to other limiting factors on weed population dynamics: a case study of *Carduus nutans*. Pages 211–219 in E. S. Delfosse, editor. Proceedings of the VII International Symposium on Biological Control of Weeds, 6–11 March 1988, Rome, Italy. Ministero dell'Agricoltura e delle Foreste Rome/ Commonwealth Scientific and Industrial Research Organisation (CSIRO), Melbourne, Victoria, Australia.
- Skarpaas, O., and K. Shea. 2007. Dispersal patterns, dispersal mechanisms and invasion wave speeds for invasive thistles. *American Naturalist* 170:421–430.
- van Groenendael, J. M., H. de Kroon, S. Kalisz, and S. Tuljapurkar. 1994. Loop analysis: evaluating life history pathways in population projection matrices. *Ecology* 75: 2410–2415.
- Wardle, D. A., K. S. Nicholson, M. Ahmed, and A. Rahman. 1995. Influence of pasture forage species on seedling emergence, growth and development of *Carduus nutans*. *Journal of Applied Ecology* 32:225–233.
- Woodburn, T. L. 1996a. Interspecific competition between *Rhinocyllus conicus* and *Urophora solstitialis*, two biocontrol agents released in Australia against *Carduus nutans*. Pages 409–415 in V. C. Moran and J. H. Hoffman, editors. Proceedings of the IX International Symposium on Biological Control of Weeds. University of Capetown, Capetown, South Africa.
- Woodburn, T. L. 1996b. Reduction of seed set in nodding thistle (*Carduus nutans*) by the seed-fly, *Urophora solstitialis*, in Australia. Pages 165–169 in B. A. McPheron and G. Steck, editors. Fruit fly pests: a world assessment of their biology and management. St. Lucie Press, Delray Beach, Florida, USA.
- Woodburn, T. L. 1997. Establishment in Australia of *Trichosirocalus horridus*, a biological control agent for *Carduus nutans*, and preliminary assessment of its impact on plant growth and reproductive potential. *Biocontrol Science and Technology* 7:645–656.
- Woodburn, T. L. 2000. Effectiveness of *Trichosirocalus horridus* against *Carduus nutans* in Australia. Page 780 in N. R. Spencer, editor. Proceedings of the Xth International Symposium on the Biological Control of Weeds. Montana State University, Bozeman, Montana, USA.