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REPORT

Interactions between density-dependent processes, population dynamics and control of an invasive plant species, *Tripleurospermum perforatum* (scentless chamomile)

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Abstract

Tripleurospermum perforatum is an invasive weedy species which exhibits strong over-compensating density dependence. Interactions between density-dependent survival, probability of flowering and fecundity were modelled and their impact on the population dynamics were examined. When only fecundity was density-dependent, the dynamics were similar to those observed in the model containing all three density-dependent terms. Density-dependent survival was a stabilizing process when acting in combination with density-dependent fecundity and probability of flowering; removing density-dependent survival from the model produced two-point cycles. The addition of a seed bank was also stabilizing. Simulations of control strategies at different life-history stages indicated that full control would be difficult due to the strong over-compensating density dependence, with severe reductions in fecundity and late season survival necessary in order to reduce equilibrium seed density and biomass.

Keywords

Equilibrium seed density, fecundity, population model, probability of flowering, simulation, survival.

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INTRODUCTION

Most plant populations are believed to exhibit stable, non-oscillatory dynamics due to fundamental aspects of their biology (Rees & Crawley 1989, 1991; Crawley 1990). There are several stabilizing processes, including the presence of a soil seed bank (Watkinson 1980; Pacala & Silander 1990; Jarry *et al.* 1995), phenotypic plasticity and asymmetric competition (Palmblad 1968; Weiner 1985; Crawley 1990; Pacala & Weiner 1991; Silvertown 1991), small size thresholds for reproduction (Rees & Crawley 1989) and self-thinning (Watkinson 1980; Watkinson & Davy 1985). Oscillatory or cyclic plant population dynamics have rarely been observed in natural populations (Symonides 1983; Symonides *et al.* 1986), although Crone (1996) demonstrated cyclic dynamics in populations of plants in a greenhouse environment. The search for oscillatory dynamics has led to interest in potentially destabilizing processes, such as over-compensating density-dependent fecundity (Thrall *et al.* 1989), time lags caused by maternal effects (Crone 1997) and large size thresholds for reproduction (Thrall *et al.* 1989).

It has long been recognized that density dependence plays a crucial role in population dynamics and, as mentioned above, can be either stabilizing or destabilizing. Density dependence refers to the way in which growth, mortality and fecundity schedules change due to fluctuations in the density of a species. Over-compensating density dependence refers to a situation in which high population densities lead to reductions in growth, mortality or fecundity through intraspecific competition, resulting in reduced densities in the following generation. Density dependence has been investigated in relation to its influence on different life-history processes in plant populations. Density-dependent fecundity and survival have been observed most frequently (Yoda *et al.* 1963; Palmblad 1968; Watkinson 1980; Symonides 1983; Thrall *et al.* 1989; Watkinson *et al.* 1989; Matthies 1990; Jarry *et al.* 1995), but density-dependent flowering phenology, out-crossing (Schmitt *et al.* 1987), seedling recruitment (Watkinson *et al.* 2000) and dispersal (Baker & O'Dowd 1982) have also been recorded.

A thorough understanding of the occurrence and effects of density dependence at different stages has been called for by several authors (Mortimer *et al.* 1989; Watkinson *et al.* 1989; Gillman *et al.* 1993). This is especially relevant for weed species where density is manipulated at one or more stages for control purposes. In order to fully understand the outcomes of these manipulations on population dynamics, we need to tease apart the interactions between density-dependent processes acting on different life-history stages. However, the stabilizing or destabilizing role of density-dependent processes operating at different times in the plant life-cycle has rarely been investigated (but see Gillman *et al.* 1993 and Lintell Smith *et al.* 1999), and the interactions between density-dependent processes have never been examined in detail.

The aims of this paper are to quantify the density-dependent processes acting in populations of the weed *Tripleurospermum perforatum* (scentless chamomile) using experimental data and to examine the effects of the different types of density dependence (acting alone and interacting) on population dynamics and control strategies. The processes explored were survival, the probability of flowering and fecundity; these were modelled as non-linear functions parameterized from experimental data. We then used these functions to construct first-order difference equation models of the system. The effects of each density-dependent process and the interactions between different processes on the predicted dynamics and equilibrium population sizes were then determined. Sheppard *et al.* (1988) have called for a greater understanding of the population dynamics of invasive species in their native range as a way of unravelling the effects of control strategies from other limiting factors. The implications of the effects of density dependence for the control of this species are discussed.

POPULATION BIOLOGY OF *T. PERFORATUM*

Scentless chamomile (*Tripleurospermum perforatum* (Mérat) Laínz, syn: *Matricaria perforata* Mérat, Asteraceae: Anthemideae) is a plant of European origin that became naturalized in North America at the end of the 19th century (Woo *et al.* 1991). It is a ruderal species that typically grows along roadsides, in drainage ditches, on farmyards, wastelands or on cropland (Hegi 1987). Two cytotypes exist in both the native and exotic ranges, diploid and tetraploid, with diploid plants predominating in maritime areas, while tetraploid plants have a mainly continental distribution (Woo *et al.* 1991; Kay 1994). The weed is reported to be phenotypically plastic and may grow as an annual, biennial or a short-lived perennial (Hegi 1987; Woo *et al.* 1991). However, in arable crops, *T. perforatum* will mostly behave as an annual because it is constrained to complete its life-cycle within one cropping period. Seeds have no obligatory dormancy period and most germinate in spring or autumn (Roberts & Feast 1974). One plant produces from a few hundred to about 200 000 seeds (Kay 1994; Blackshaw & Harker 1997; Hinz 1999). However, large plants that grow under optimal conditions may produce over one million seeds (Woo *et al.* 1991; Kay 1994), and seed banks of up to 100 000 seeds per m^2 were found in Canada within dense stands (Douglas 1989).

METHODS

Field experiment

The experiment was carried out in the German Rhine Valley (47°48′N, 7°37′E) in a fallow field where scentless chamomile had not occurred in recent years. Density-dependent processes were investigated by sowing seeds of scentless chamomile on September 3rd 1993 at five different densities (10, 100, 1000, 10 000, 25 000) in 50 × 50 cm plots. The highest density corresponded to the maximum seed bank counts reported (see above). Because diploid and tetraploid populations of scentless chamomile converge in the Rhine Valley (Kay 1969), it is not known which cytotype occurred, but preliminary data suggest that most populations are tetraploid (H.L. Hinz, unpublished data).

Five replicates were set up per density. In the three lower density plots, all emerging seedlings were counted and marked, while in the two higher density plots, seedlings were only counted in three subplots (10 × 10 cm). The plots were censused four times, once in late autumn 1993 and three times during the growing season in 1994. From July until mid-September, ripe seed heads were collected at regular intervals, separately from each plot. The seeds were cleaned and the germination rate was determined for 100 seeds per plot. To estimate the number of seeds produced, five replicates of 100 seeds were counted and weighed per plot. At the end of September, all plants were uprooted and the dry weight (24 h at 70 °C) of below- and above-ground biomass was recorded. The survival probability was determined by the proportion of seeds sown that survived to the flowering season (approximately 11 months), and the flowering probability was determined as the proportion of surviving plants which flowered. Average fecundity was only determined for plants which flowered.

Model development

A winter annual life-cycle was assumed, with seeds germinating in the autumn, developing into rosettes and flowering the following summer. This assumption applies to a cultivated habitat (e.g. wheat fields) where flowering scentless chamomile plants senesce naturally after setting seed and the remaining plants are destroyed during harvest and subsequent cultivation. There was therefore assumed to be no carry-over of biennials from one year to the next. Two types of model were constructed: model 1 is based on the hyperbolic competition model (Hassell 1975; Watkinson 1980) and does not partition density dependence among different life-history events; model 2 partitions density dependence among each of the following: survival, flowering probability and fecundity per flowering plant. Parameterized functions describing the density dependence at each of the stages were estimated using the experimental data. Our partitioned model (model 2) was compared to the traditional approach (model 1) in order to see if the predicted dynamics differed and to investigate the utility of partitioning the different components of density dependence.

Quantitative data on seed bank dynamics were not collected during this study; this precluded detailed modelling of the seed bank dynamics. To assess the effect of a seed bank on the population dynamics, we used data from a different experiment conducted in the same region, in which it was estimated that about 2% of seeds produced became incorporated into the soil seed bank (Hinz 1999). As reported data on the incorporation of seeds into the seed bank are variable (e.g. Bowes *et al.* 1995), we examined the inclusion of higher seed bank incorporation values (20% and 50%) to assess the effect of larger seed banks on the population dynamics. This was performed by adding the term (kS_t) to all models, where k represents the proportion of year t seed which was held in the seed bank and available for germination the following year. The inclusion of a seed bank of any size was a stabilizing force, but did not affect the qualitative population dynamic behaviour of any of the models. For these reasons, the seed bank term was omitted from the models below to enable us to more clearly present the interactions between density-dependent terms.

Model 1

A first-order difference equation was used to describe the overall pattern of density dependence, ignoring different stages in the life-cycle of the plant. The model used was Hassell's (1975) model, namely

$$S_{t+1} = S_t \lambda (1 + aS_t)^{-b} \tag{1}$$

where S_t and S_{t+1} indicate the total seed present in successive generations and λ, a and b are fitted parameters. Stability analysis (Hassell 1975) indicates that the model can produce a wide range of dynamics from a stable equilibrium through population cycles and chaos. The condition for neighbourhood stability is $2 > b(1 - \lambda^{-1/b}) > 0$. Therefore, the key parameters determining the stability of the model are λ and b (Hassell 1975).

Model 2

In this model, three density-dependent life-history events were modelled. The events occur in the following order: survival, probability of flowering and seed production. Due to constraints in the data, the survival function is modelled as the proportion of seeds sown that produce a flowering plant; this incorporates several life-stages and is a simplification of the processes acting on seedlings, young and mature plants. After extensive exploratory data analysis, the following functions were found to describe the data well. For survival and probability of flowering, we used versions of the logistic model, namely

$$p_{\mathrm{s}} = 1/(1 + \mathrm{e}^{c + d \ln S_t}) \tag{2a}$$

and

$$p_{\mathrm{fl}} = [\mathrm{e}^{g}(S_t p_{\mathrm{s}})^{-h}]/[1 + \mathrm{e}^{g}(S_t p_{\mathrm{s}})^{-h}] \tag{2b}$$

where p_{s} is the probability of survival to reproduction and p_{fl} is the probability of flowering. The parameters c, d, g and h are estimated parameters that describe the density-independent and density-dependent effects. The fecundity per flowering plant was described using a hyperbolic relationship of the form

$$f = F_{\max}/[1 + i(S_t p_{\mathrm{s}})]^{j} \tag{3}$$

where f is the fecundity per flowering plant, $F_{\max}$ is the maximum number of seeds produced by a plant in the experiment and i and j are fitted parameters.

Using these three functions, we can write down a discrete time, first-order difference equation describing the dynamics, namely

$$S_{t+1} = S_t p_{\mathrm{s}} p_{\mathrm{fl}} f \tag{4}$$

The resulting model cannot be solved analytically and so the dynamics were explored using numerical simulation. In order to thoroughly explore the range of transient behaviour, starting values for S_t spanning the entire range of possible values were used (i.e. 1, 250 000, 1 000 000 and 2 000 000).

Deconstructing density dependence

Density-independent parameter estimates for all three life-history stages were determined by setting S_t (number of seeds sown) to unity in each of the density-dependent functions (eqns 2a,b and 3) (see Table 1). These estimates were substituted for the density-dependent functions one at a time, and in all two-way combinations, in order to investigate the influence of different types of density dependence, and the interactions between them, on the behaviour of model 2.

Control

The implications of the results of these models for the control of *T. perforatum* were investigated by looking at how reductions in fecundity and survival would affect equilibrium population size and biomass. For fecundity, $F_{\max}$ (maximum fecundity per plant) was reduced in small steps in order to plot the response of the equilibrium population size

Table 1 Parameter estimates, standard errors (SE) and R^2 values for models 1 and 2. Density-independent parameter estimates are also given.

Model 1				Model 2					Density-independent estimates	
Parameter	Estimate	SE	R^2	Function	Parameter	Estimate	SE	R^2	Parameter	Estimate
$\ln \lambda$	10.759	0.296	0.99	p_s survival	c	−2.085	0.09	0.7	p_s survival	0.89
a	0.054	0.024			d	0.481	0.009			
b	1.205	0.049		p_{fl} flowering	g	7.532	0.389	0.74	p_{fl} flowering	1
					h	0.883	0.054			
				f fecundity	F_{max}*	62 000		0.98	f fecundity	58 419
					i	0.053	0.014			
					j	1.305	0.081			

*F_{max} is the maximum number of seeds produced by a plant in the experiment.

and biomass. Three different types of density-independent (additional) mortality were examined:

1 early mortality, where control occurs before density-dependent mortality;

2 established plant mortality, where control occurs in an established stand where density-dependent mortality has already occurred;

3 late mortality, where control occurs after flowering (but before seed set).

Statistical methods: estimation of model parameters

Non-linear regression was used to obtain parameter estimates of the different models. Eqns 1 and 3 were fitted by least-squares assuming a normal error distribution. As the survival and flowering functions (eqns 2a and 2b) were based on the logistic equation, they were fitted using maximum likelihood estimation assuming the data were drawn from a binomial distribution (McCullagh & Nelder 1989). When we fitted eqn 1, we modelled the logarithmic growth rate ($\ln(S_{t+1}/S_t)$) as a function of the sowing density, S_t.

RESULTS

Fitted functions

Model 1 was found to provide a good fit to the overall pattern of density dependence (see Table 1 for parameter estimates and R^2 values, and Fig. 1a). The parameter estimates of the fitted functions in model 2 are also given in Table 1 (data and fitted functions are given in Fig. 1b–d).

Population dynamics

Both models provide a good fit to the overall pattern of density-dependent seed production (Fig. 1a). The models both exhibit damped oscillations, and have similar predicted equilibrium levels (model 1, 143 963 seeds/plot; model 2, 139 702 seeds/plot). In both models, the damped oscillations originate from the steep negative gradient in the latter half of the seed production curve (see Fig. 1a). The key question, then, is why does the seed production curve have a steep negative gradient? We addressed this question by systematically removing different forms of density dependence from model 2 and exploring the resulting dynamics.

Density dependence in either survival or flowering probability alone proved to be weak, and the dynamics showed a monotonic increase to very high equilibrium densities (see Table 2). The combination of density-dependent survival and flowering probability also exhibited a monotonic approach to an equilibrium higher than the equilibrium of the fully density-dependent model. Interestingly, the combination of density-dependent flowering probability and fecundity produced two-point cycles (see Fig. 2). This appears to be due to the destabilizing effect of the probability of flowering declining at very high densities. At high densities, few plants flower and those that do produce few seeds. The following year these few seeds are released from density dependence, resulting in rapid rates of population increase, so producing the two-point cycles. However, density-dependent survival is a stabilizing force which, when added to the unstable fecundity/flowering probability model, removes the two-point cycles. The reason for this is that density-dependent mortality prevents the population from reaching high densities where seed production is over-compensating, so preventing a population crash.

Control

Reduction in fecundity did not decrease biomass until over 90% reductions were imposed; however, equilibrium seed density decreased with decreasing fecundity (Fig. 3c). Both early and established plant mortality showed no decline in biomass until over 90% reductions were imposed. In addition, with early mortality, equilibrium seed density actually increased up to the 90% additional mortality level

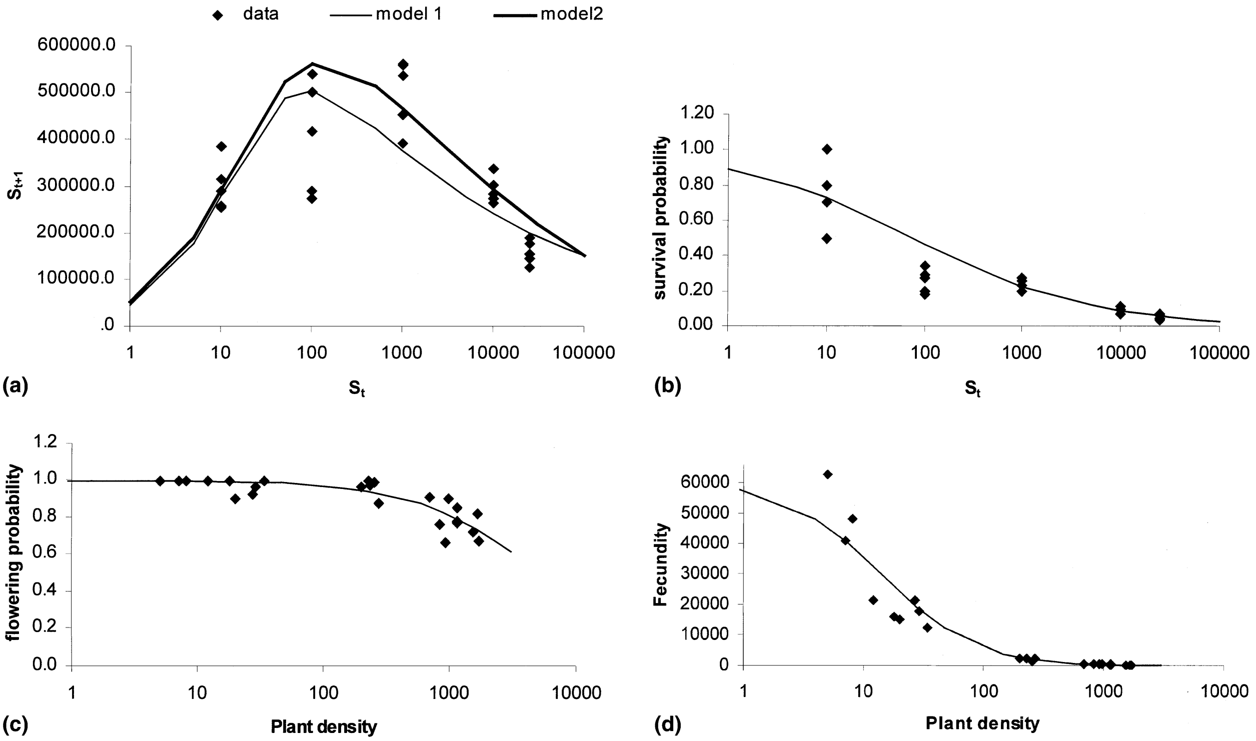

Figure 1 (a) Comparison of experimental data (filled diamonds) with model 1 (light line) and model 2 (heavy line). (b) Probability of survival to flowering season (as a function of seeds sown). (c) Flowering probability (as a function of total plant density in the flowering season). (d) Per flowering plant fecundity (as a function of total plant density in the flowering season). For (b)–(d), experimental data (filled diamonds) and fitted density-dependent functions (line) are shown.

Table 2 Population dynamics and equilibrium seed production values, including density dependence singly, in all pairwise interactions and the full models 1 and 2.

Density-dependent process(es)	Dynamics	Equilibrium value	Difference from full model equilibrium
Survival	Monotonic increase to equilibrium	619 733 359 719	+619 733 215 756
Flowering	Monotonic increase to equilibrium	1 336 001 160	+1 335 857 197
Fecundity	Damped oscillations	91 155	−52 808
Survival + flowering	Monotonic increase to equilibrium	469 417 454	+469 273 491
Survival + fecundity	Damped oscillations	217 169	+73 206
Flowering + fecundity	Oscillations turning into two-point cycles	41 845, 17 368	−102 118, −126 595
Flowering + fecundity + survival	Damped oscillations	143 963	0

(Fig. 3b); this is due to the few plants surviving producing a much larger amount of seed than a population where density-dependent fecundity is allowed to act and reduce seed production. Only late mortality resulted in a decrease in biomass over the range of mortality levels and equilibrium seed density also decreased (Fig. 3a).

DISCUSSION

The model incorporating only density-dependent fecundity most closely resembles the most complex version of model 2, including density-dependent fecundity, mortality and flowering probability, and it also exhibits similar dynamics to model 1 which combines all sources of density dependence. This demonstrates that strong density-dependent fecundity drives the dynamics of the population, causing damped oscillations; this is in line with the findings of others who have shown that a humped density–seed set relation, resulting in over-compensating density dependence, can destabilize dynamics (Pacala & Silander 1985; Symonides *et al.* 1986; Thrall *et al.* 1989).

Scentless chamomile is a facultatively biennial species and appears to show a tendency to delay flowering, switching to a biennial life-style at high densities. Although plants were

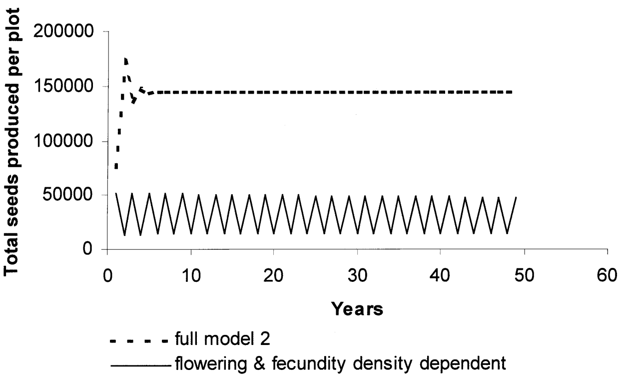

Figure 2 A model combining density-dependent probability of flowering and per capita fecundity with a density-independent estimate of survival (full line) produces two-point cycles; it is shown here compared with the fully density-dependent model 2 (broken line).

not followed for a second year, the non-flowering plants present at high densities would have presumably flowered in the following year. This negative density-dependent probability of flowering has the potential to destabilize the population dynamics further, as seen by the production of two-point cycles when combined in the model with density-dependent fecundity. However, the inclusion of density-dependent survival ensures that the population never reaches high enough densities for a large decrease in the probability of flowering to exacerbate the over-compensation apparent in the fecundity function (as seen by the stabilizing affect of adding density-dependent survival to the previous model). The addition of a soil seed bank to our models was stabilizing. Similarly, the addition of seed dormancy had a stabilizing effect in the model of Thrall *et al.* (1989). In addition, germination success has been shown to be critical in determining population dynamics in populations with over-compensating density-dependent fecundity (Symonides *et al.* 1986; Thrall *et al.* 1989).

Strong density-dependent fecundity has been shown to cause oscillations in annual plant species (Symonides *et al.* 1986; Thrall *et al.* 1989) due to a humped relationship between density and seed set. The nature of the oscillations is determined by the magnitude of the negative slope on the density–seed set curve. Our study differs in that we split per capita reproductive success into two density-dependent processes, flowering probability and a per flowering plant fecundity, showing that it is the interaction between these components which controls the dynamics. Density-dependent flowering probability can be viewed as a more general form of the process of size-dependent flowering observed in Thrall *et al.*'s populations where, at high density, most plants in their study population were small and some were so small that they were unable to reproduce.

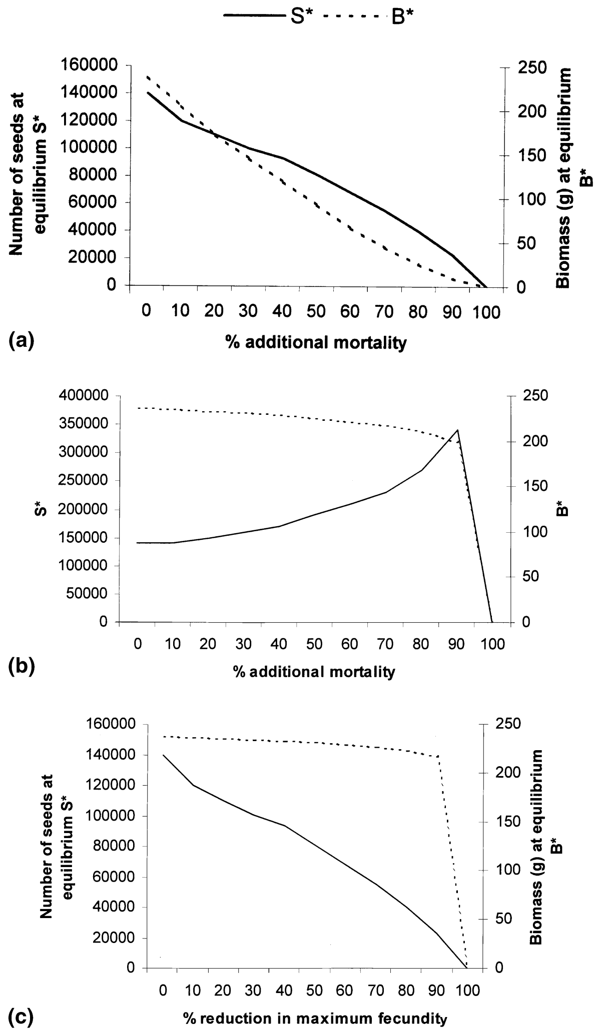

Figure 3 Effect of control strategies on the equilibrium seed production and biomass: (a) effect of additional mortality imposed late in the growing season, post-flowering; (b) effect of early mortality imposed before density-dependent survival; (c) effect of reducing fecundity.

For facultative biennials, such as *T. perforatum*, the adoption of an annual or biennial strategy will depend on the fitness achieved by flowering in the first year in comparison with the fitness achieved by flowering in the second year, where the plants may be at a competitive advantage over first year plants; this is of course discounted by the cost of surviving for an extra year. More data on the full life-cycle of biennials is required in order to model the optimal flowering strategies at different densities and mixtures of first and second year plants, and to predict the dynamics of a mixed population. This is also of relevance to populations in the exotic range where scentless chamomile inhabits uncultivated sloughs or field margins and where low tillage cultivation is used. In these cases, the survival of adult plants may be extended into their second year, and understanding the biennial life-cycle becomes especially important. In addition, Freckleton & Watkinson (1998) and Freckleton *et al.* (2000) showed that the strength of competitive interactions (both intra- and interspecific) may be affected by the timing of emergence of weed seedlings. The experiment described in this paper used sown seed; therefore, the emergence of seedlings will be more synchronous than that expected in a naturally regenerating population, leading to more unstable population dynamics than in a population in which asymmetric competition is stronger. We would therefore expect asymmetric competition to be an additional stabilizing factor in the population dynamics of field populations of this species, especially where there is some carry-over of biennials from one year to the next.

A greater understanding of weed population dynamics has been called for in an effort to formulate economically viable and sustainable methods of control (Mortimer *et al.* 1989; Lonsdale 1996). The efficacy and success of the control measures will depend to a large extent on how the population size of the weed is determined. Part of the determination of population size will be density-independent (e.g. weather, harvesting, etc.) and part will be due to density-dependent processes and competition from other species, including the crop. Control measures will occur at one or more of the life-stages of the species, and the response of the population over future generations will depend to some extent on whether density dependence at that stage is over-, under- or exactly compensating. The control measures themselves may operate in a density-dependent or density-independent way and, for weed management, it is important to determine "if control measures themselves are likely to generate patterns of population behaviour that, over generations of weeds, …cause intrinsic fluctuations in abundance" (Mortimer *et al.* 1989). The steps to achieve this aim consist of:

1 the detection and partitioning of density dependence among the different life-stages of the weed;

2 the determination of the contribution of the components of density dependence to the population dynamics;

3 the examination of the behaviour of the population in response to different management regimes.

We have shown here that management regimes likely to be effective will have to incorporate severe and sustained reductions in fecundity and reductions in survival late in the growing season. Strongly over-compensating density dependence can actually exacerbate a bad infestation if plants are removed early in the growing season. Similar results were obtained for *Centaurea diffusa*, where an 80% reduction in rosette density in spring was compensated for in autumn in two out of three populations, and seedling survival increased (Myers *et al.* 1990). The control models presented are based on models which do not have a seed bank component; for this reason, control of scentless chamomile is likely to be even more difficult to achieve than presented here. However, these models represent annual monospecific populations; better control might be achieved where interspecific competition is present and is more severe than intraspecific competition. The inclusion of a crop, for example, could further tend to stabilize dynamics by reducing fecundity and the proportion of flowering plants.

The utility of population models in predicting dynamics has been questioned (Cousens 1995) and the need for realistic models and parameter values has been stressed. Cousens (1995) and Gonzalez-Andujar & Hughes (2000) point out that one of the problems with simple models is that different functions could fit the data equally well, but yet produce widely differing dynamics. In this paper, we have demonstrated an alternative approach to using a simple model of the seed production curve which incorporates several density-dependent stages. We show that, by careful decomposition of the density dependence, the predictions of different models can be disentangled.

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BIOSKETCH

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