Stable coexistence of an invasive plant and biocontrol agent: a parameterized coupled plant–herbivore model

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Summary

1. Coupled plant–herbivore models, allowing feedback from plant to herbivore populations and vice versa, enable us to predict the impact of biocontrol agents on their target weed populations; however, they are rarely used in biocontrol studies. We describe the population biology of the invasive plant *Echium plantagineum* and the weevil *Mogulones larvatus*, a biocontrol agent, in Australia. In order to understand the dynamics of this plant–herbivore system, a series of coupled models of increasing complexity was developed.
2. A simple model was extended to include a seed bank, density-dependent plant fecundity, competition between weevil larvae and plant tolerance of herbivory, where below a threshold plants could compensate for larval feeding. Parameters and functional forms were estimated from experimental and field data.
3. The plant model, in the absence of the weevil, exhibited stable dynamics and provided a good quantitative description of field densities before the weevil was introduced.
4. In the coupled plant–herbivore model, density dependence in both plant fecundity and weevil larval competition stabilized the dynamics. Without larval competition the model was unstable, and plant tolerance of herbivory exacerbated this instability. This was a result of a time delay in plant response to herbivore densities.
5. *Synthesis and applications.* The coupled plant–herbivore model allowed us to predict whether stable coexistence of target plant and biocontrol agents was achievable at an acceptable level. We found this to be the case for the *Echium–Mogulones* system and believe that similar models would be of use when assessing new agents in this and other invasive plant biocontrol systems. Density dependence in new biocontrol agents should be assessed in order to determine whether it is likely to result in the aims of classical biocontrol: low, stable and sustainable populations of plant and herbivore. Further work should be done to characterize the strength of density dependence according to the niche occupied by the biocontrol agent, for example the strength and functional form of density dependence in stem borers may be quite different to that of defoliators.

Key-words: biological control, density dependence, herbivore tolerance, integrated weed management, *Mogulones larvatus*, Nicholson–Bailey model, structural uncertainty

Introduction

The aim of classical biocontrol is to introduce a control agent that will reduce and sustain the target population

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at an environmentally or economically acceptable level. In order to improve the success rate of biological control programmes in general, and to reduce the environmental risks of introducing unnecessary biocontrol agents (Simberloff & Stiling 1996), we need to be able to assess which control agents are likely to have an effective impact on the target weed. Coupled plant–herbivore models, where there is a feedback loop between plant and herbivore populations, enable us to assess whether the plant–herbivore interaction is likely to be stable and what

reduction in weed density is achievable by the biocontrol agent. However, despite this potential, a review of the use of models in biocontrol found that all of the weed–herbivore models examined concentrated solely on the plant dynamics, ignoring herbivore dynamics (Barlow 1999).

Coupled discrete time models for host–parasitoid interactions have a long history of use in ecology (Nicholson & Bailey 1935; Hassell 1978) and, in an applied context, biocontrol of insect pests with parasitoids (Barlow 1999). These models incorporate the feedback between host and predator dynamics that is essential for understanding long-term dynamics. Biologically realistic aspects of demography, such as density dependence and invulnerable life-history stages, can be incorporated easily into the basic model in order to explore their effects on population persistence and stability, and to make more realistic predictions of the outcome of specific interactions (Gurney & Nisbet 1998). These discrete time models are suitable for annual systems where both the plant and herbivore complete their life cycles within one generation, as is the case for the invasive pasture plant *Echium plantagineum* and the introduced biocontrol agent *Mogulones larvatus* in Australia.

Even in the general ecological literature there are few studies of discrete time coupled plant–insect herbivore systems (Gurney & Nisbet 1998; van der Meijden, Nisbet & Crawley 1998). Several papers have explored the impact of a biocontrol agent whose dynamics are not coupled to the plant dynamics (Crawley 1983; Watkinson, Lonsdale & Andrew 1989; Lonsdale, Farrell & Wilson 1995; Rees & Paynter 1997; Shea & Kelly 1998; Rees & Hill 2001; Buckley *et al*. 2004). Other studies have assumed that plant dynamics are independent of the herbivore population, and have explored herbivore persistence and dynamics (Lakhani & Dempster 1981; Gillman & Crawley 1990; Halley & Dempster 1996). There is, however, an extensive literature on continuous time plant–herbivore models (May 1974; Noy-Meir 1975; Caughley & Lawton 1981), a large and growing literature dealing with plant–herbivore dynamics in aquatic systems (Gurney *et al*. 1990; Nisbet *et al*. 1991; McCauley *et al*. 1999) and good examples of coupled plant–mammalian herbivore systems (Turchin 2003).

While considerable work on plant–herbivore systems has focused on the widespread occurrence of plant tolerance, the ability of plants to withstand herbivory through compensatory growth (Strauss & Agrawal 1999 and references therein), little work has been undertaken to explore the effects of plant tolerance on the population dynamics of plant–herbivore systems (Juenger & Lennartsson 2000; for community effects of tolerance see Chase, Leibold & Simms 2000). Tolerant plants do not respond immediately to increased numbers of herbivores; there is a threshold below which no effect of herbivores on plant fitness is felt. There may therefore be a jump from no effect to considerable effect as that threshold is passed, possibly leading to more unstable dynamics than a smooth continuous decline in plant

fitness with increasing herbivore numbers. However, until now, there have been no quantitative studies exploring the consequences of plant tolerance on abundance and dynamics of a plant–herbivore system.

In this study we explored the interaction between *E. plantagineum* and the introduced biocontrol agent *M. larvatus* using coupled discrete time plant–herbivore models. Starting with a basic model we successively incorporated more realistic features of the *Echium–Mogulones* system, such as a seed bank and density dependence in both plant and herbivore populations and plant tolerance of herbivory. The models were parameterized and compared with both experimental and field data. We explored the population dynamics of both plant and herbivore and investigated which features of the interaction were stabilizing, using stability analyses of the simpler models to explain the dynamics of more complex simulation models.

Echium–Mogulones demography

Echium plantagineum (Boraginaceae) is a winter or cool-season annual typical of annual-dominated pasture communities on neutral to acid sandy soils in Mediterranean-type climates (Noy-Meir, Gutman & Kaplan 1989; Fernández Alés, Leiva & Laffarga 1991; Piggin & Sheppard 1995). Native to the western Mediterranean, *E. plantagineum* has been introduced to Australia, South America, South Africa and parts of Asia, where in pasture communities it can often become dominant, causing alkaloid toxicity for grazing livestock. Germination of the relatively large seeds (360–390 mg) is controlled by moisture and temperature and is favoured by relatively high constant (20–30 °C) or alternating (15 °C/40 °C) temperatures (Piggin & Sheppard 1995). This typically leads to one or several seedling cohorts following summer and autumn rains, which survive through winter as rosettes until mid-spring. At this time a crowded paniculate inflorescence is produced that flowers for about 2 months (Piggin & Sheppard 1995). Variation in rosette survival is related to germination time; the earlier summer cohorts often suffer higher mortality as a result of drought (Burdon, Marshall & Brown 1983). Survivors tend to be larger, however, having higher fecundity than individuals from later cohorts. Seed production is proportional to plant weight (Sheppard, Smyth & Swirepik 2001) and there is no size requirement for flowering (A. Sheppard & M. Smyth, unpublished data). The seeds have an after-ripening requirement (Piggin & Sheppard 1995) and become incorporated into a seed bank, from which roughly 15% of seeds can recruit as seedlings each year (Grigulis 1999). Mean values for various population parameters in grazed pastures from three sites in Australia between 1989 and 1997 (Grigulis 1999; Grigulis *et al*. 2001) are given in Table 1.

In its native range, *E. plantagineum* is intermittently attacked by the univoltine, root-crown weevil *M. larvatus* (Sheppard, Smyth & Swirepik 2001). Newly emerged

Table 1. Parameters for *E. plantagineum* in grazed pastures in Australia. Means and standard errors or range

Parameter description	Symbol	Value	Source
Plant density-dependence shape parameter	a	0·1	1
Herbivore tolerance damage function shape parameter	α	0·0216 ± 0·008	Results
Weevil attack rate (eggs/plant/weevil)	a_w	0·01–0·5	Appendix 2
Conversion coefficient for fecundity to biomass	c	0·025	3,4
Seed bank decay (excluding recruitment)	d	0·15–0·35	2,3
Maximum plant fecundity	F	660 ± 99	2, 3
Recruitment of seed in seed bank to seedling	g	0·13 ± 0·02	2, 3
Seed incorporation rate into seed bank	l	0·30–0·60	2, 3
Herbivore tolerance damage function intercept	p_s	2·21 ± 0·71	Results
Seedling survival to flowering	s	0·30 ± 0·03	2, 3
Larval survival, shape parameter (contest competition)	u	0·02 ± 0·04	Fig. 6
Larval survival, shape parameter (scramble competition)	u	0·012 ± 0·009	Fig. 6
Simple damage function shape parameter	v	0·014 ± 0·002	Results
Larval survival, intercept (contest competition)	w_s	0·57 ± 0·45	Fig. 6
Larval survival, intercept (scramble competition)	w_s	0·5 ± 0·2	Fig. 6
Shoot biomass	B	cF	
Density dependent shoot biomass	B_t	$cF/(1 + agsS_t)$	
Proportion of seeds remaining in the seed bank	ρ	$(1 - d)(1 - g)$	
Plant dens. dependent parameter/(weevil larvae per plant)	ϕ	$al/(a_w w_s)$	
Plant basic reproductive rate	R_0	$gsFl$	
Plant basic reproductive rate with a seed bank	R_{0SB}	$gsFl/(1 - \rho)$	

1, Grigulis (1999); 2, Grigulis *et al.* (2001); 3, A. Sheppard *et al.*, unpublished data; 4, Sheppard, Smyth & Swirepik (2001).

adults appear from the soil in spring, feed on the flowering *E. plantagineum* plants, and then aestivate over summer in the soil and leaf litter. The weevils become active again after 3–5 months aestivation or late summer/autumn rains, emerging over a 2–3-month period. Adult females then search for, and feed on, fresh rosette leaves and oviposit in the leaf axils. The oviposition period lasts throughout the remaining 8 months of the growth cycle of the plant. Oviposition rates vary between one and six eggs female^{-1} day^{-1}, only being curtailed when winter temperatures drop below 5 °C. Using individual pairs of weevils in controlled temperature rooms, mean female lifetime fecundity was measured as 448 ± 38 (mean ± SE, range 46–899) (M. Smyth, unpublished data). Adult weevils fly on warm days and can locate host-plants several hundred metres from the point of release. There is, however, little effect of patch size and a weak negative effect of plant density on eggs laid per plant (Shea *et al.* 2000). Eggs take about a week to hatch and the larvae bore down the leaf stems into the root crown, where they complete development in about 2–6 months depending on temperature. High attack levels can lead to plant death and severe larval competition for resources.

Mogulones larvatus was found attacking *E. plantagineum* at 21 of 75 sites during a number of surveys in France, Spain and Portugal between 1987 and 1996, with the percentage of plants attacked (attack rate) ranging between 1% and 19%. This weevil is also now present in Australia, where it has been released as part of a biocontrol programme against *E. plantagineum*, and has established at 35% of more than 800 release sites. At sites where it has established, attack rates from 1% to 100% of plants have been observed. At three sites where the weevil has been established for 5 years or more, it regularly kills between 10% and 46% of plants

(Sheppard *et al.* 2002). At one site in particular, Yanco (southern New South Wales), where data on weevil numbers and attack rates were collected from 1993 to 2002, the weevil population killed the whole population of its host over 1·5 ha, preventing any seed production in 1998 and 2001 (Sheppard *et al.* 2002).

Simple homogeneous population models for the *Echium–Mogulones* system

Echium plantagineum is a winter annual that forms a seed bank. The dynamics of simple annual plant populations of this type can be represented by a model of the form (MacDonald & Watkinson 1981):

$$S_{t+1} = (1 - d)(1 - g)S_t + S_t gslf(gsS_t) \qquad \text{eqn 1}$$

where S_{t+1} is the density of seeds in the seed bank in year $t + 1$, the first term on the right is the number of seeds remaining in the seed bank and the second term is the number of seeds produced in year t that get incorporated into the seed bank. S_t is the density of seeds in the seed bank in year t, d is the probability a seed is lost from the seed bank through decay, s is the probability a seedling survives to reproduce, g is the recruitment probability, l is the probability a seed is incorporated into the seed bank, and $f(gsS_t)$ is a density-dependent fecundity term, equal to F in the absence of density dependence.

A BASELINE PLANT–WEEVIL MODEL

The weevil has two effects on plant demography: the first is a sublethal reduction in plant size, with consequent reductions in fecundity, and the second mortality

(Sheppard, Smyth & Swirepik 2001). At a weevil density of W_t we assume average plant fecundity, F, is reduced by a term $\exp(-va_wW_t)/B$, where v is a rate constant that describes how rapidly plant fecundity is reduced by weevil feeding, a_w is the weevil attack coefficient (number of eggs weevil^{-1} plant^{-1}), and B the plant biomass, given by a conversion constant, c, times average plant fecundity, F. This leads to the following baseline model:

$$S_{t+1} = (1-d)(1-g)S_t + S_tgslf(gsS_t)\exp\left(\frac{-va_wW_t}{cF}\right)$$

$$W_{t+1} = S_tgsW_ta_ww_s \qquad \text{eqn 2}$$

where w_s summarizes the density-independent mortality acting on eggs and larvae. Without a seed bank ($d = 0$) and without plant density dependence $f(gsS_t) = F$, this model is similar to the conventional Nicholson–Bailey (N-B) host-parasitoid model; in our case, however, more than one weevil can emerge from each plant, whereas in the conventional N-B model only one parasitoid can emerge from each host. As in the conventional N-B model, this equilibrium is never locally stable (see Appendix 1), thus the simplest possible annual plant–herbivore model is always unstable. The addition of a seed bank alone is not sufficient to stabilize the interaction. For a similar result from a host–parasitoid model see Ringel, Rees & Godfray (1998).

A widely used model for plant density dependence, which provides a good description of many plant populations (Watkinson 1980; Watkinson & Davy 1985; Watkinson 1990; Lonsdale, Farrell & Wilson 1995), is the hyperbolic density-dependence function $f(gsS_t) = F/(1 + agsS_t)$, where a is a parameter describing the severity of the density-dependence curve. In the absence of a seed bank, the basic reproductive rate, R_0, is the number of seeds produced on average from the introduction of a single seed and when freed from density-dependent constraints $R_0 = gsFl$ (for definitions of all parameter combinations see Table 1). In the presence of a seed bank, R_{0SB} can be calculated by summing all future reproduction, hence , $R_{0SB} = gsFl(1 + \rho + \rho^2 + \dots) = gsFl/(1 - \rho)$, where for notational convenience the carryover of seeds from one year to the next is denoted as $\rho = (1-d)(1-g)$. Clearly $R_{0SB} > 1$ implies that the population growth rate (λ) will also be positive.
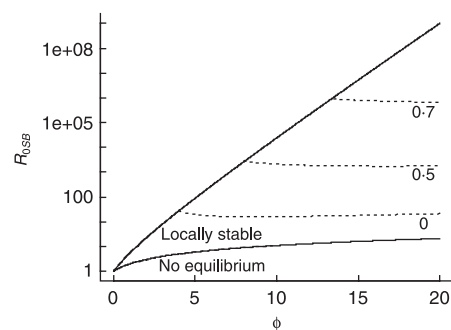
The plant model is now:

$$S_{t+1} + 1 = \rho S_t + \frac{S_tgsFl}{1 + agsS_t} \qquad \text{eqn 3}$$

In the absence of weevils this gives an equilibrium density of $S^* = (R_{0SB} - 1)/ags$, from which we find the equilibrium density of flowering plants, $P^* = gsS^*$. This equilibrium in the absence of the weevil is always stable (MacDonald & Watkinson 1981; see Appendix 1).

Incorporating the change in parameters we arrive at the following model:

$$S_{t+1} = \rho S_t + \frac{S_tgslF}{1 + agsS_t}\exp\left(\frac{-va_wW_t}{B_t}\right)$$

$$W_{t+1} = S_tgsW_ta_ww_s \qquad \text{eqn 4}$$

Fig. 1. Stability boundaries for the plant density-dependent model. On the *y*-axis is the basic reproductive rate, R_{0SB}, and on the *x*-axis is the ratio between the plant density-dependence parameter and the weevil attack coefficient, ϕ. Equilibria are locally stable within the area bounded by the solid and broken lines. The solid lines are boundaries for all parameter combinations; the numbers below the dashed lines give the proportion of seed carried over from one year to the next (ρ); an increase in the seed bank increases the area of local stability; g is set to 0·13 throughout.

Plant average biomass with density dependence, B_t, is given by $B_t = cF/(1 + agsS_t)$. The equilibrium seed bank is $S^* = 1/a_ww_sgs$, and the weevil equilibrium is given by $W^* = [cF/a_wv(1 + \phi)]\ln[R_{0SB}/(1 + \phi)]$, where $\phi = a/a_ww_s$ (Table 1), the ratio of the plant density-dependence severity parameter, a, to the effective weevil attack rate, a_ww_s. The equilibrium is locally stable providing two conditions are met. The first is $R_{0SB} < (1 + \phi)\exp\phi$, which puts a limit on the plant's basic reproductive rate, R_{0SB}, relative to the ratio ϕ (Fig. 1). The second condition is more complex (Appendix 1, equation A4) and depends on R_{0SB}, ϕ and the seed bank ρ; stability boundaries for this model are given in Fig. 1. If plant density dependence is weak (low a) or weevil impact is high (high a_w and/or w_s) leading to smaller values of ϕ, local stability can only be achieved by a narrow range of low R_{0SB} values. Increasing the parameter combination ϕ leads to an increase in the maximum value of R_{0SB} for stability, showing clearly that increasing the severity of plant density dependence, or decreasing weevil impact (up to a maximum), leads to a wider region of stability. The range of parameters that are locally stable increases as the carryover of seeds in the seed bank, ρ, increases. In summary, plant density dependence is sufficient to stabilize the interaction, and increasing the seed bank carryover increases the area range of parameter values where the model is locally stable.

INCORPORATING WEEVIL DEMOGRAPHY

The models described above assume weevil larvae do not compete within the root crown; we now relax this assumption. We explore two types of density-dependent functions describing competition between larvae. The first assumes contest competition between larvae and uses the following function:

$$p(\text{survival}) = \frac{w_s}{1 + ua_w W_t / B} \qquad \text{eqn 5}$$

where the parameter u describes how rapidly larval survival decreases with density per unit plant biomass, and B is average plant biomass. In the second, when competition is scramble in form we use the function:

$$p(\text{survival}) = w_s \exp(-ua_w W_t / B) \qquad \text{eqn 6}$$

For examples of the use of these models in host–parasitoid models, see Taylor (1988). As we cannot perform stability analysis for a model including both plant and herbivore density dependence to explore the effects of larval competition, we assume the plant forms a seed bank but plant performance is density independent. This leads to the following condition for local stability:

$$(1 - \rho)(v/u + \ln R_{0SB}) < 1 \qquad \text{eqn 7}$$

Forming a seed bank in general makes this condition easier to satisfy, as the parameter combination $1 - \rho$ becomes small (Fig. 2a). Increasing the germination rate destabilizes the interaction because it decreases ρ while increasing $R_{0SB.}$

Changing the form of competition to scramble leads to the stability conditions outlined in Appendix 1 (equations A9 and A10). The second condition, equation A10, is violated if v/u is sufficiently small; like the contest competition model, this means that scramble competition can stabilize the interaction providing competition is not too strong (u is large if competition is strong; Fig. 2b).
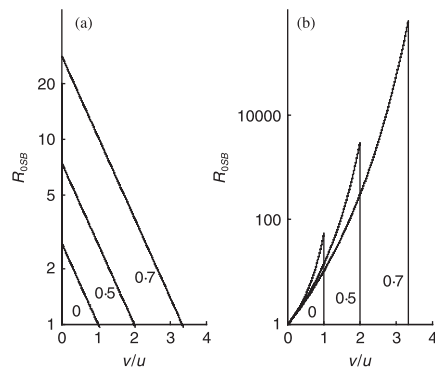
Fig. 2. Stability boundaries for the weevil competition models (without plant density dependence). On the *y*-axis is the basic reproductive rate, R_{0SB}, and on the *x*-axis is the ratio between v, the simple damage function shape parameter, and u, the larval survival shape parameter. (a) Stability boundaries for the contest competition model; parameter space to the left of the boundaries is stable; stability area increases with the size of the seed bank ρ; the model is stable only at low values of R_{0SB}. (b) Stability boundaries for the scramble competition model; parameter space within the boundaries is stable and increases with the size of the seed bank ρ; however, as v/u decreases stability area also decreases.

Parameter estimation and model predictions

In this section we use data from a number of sources to parameterize the models and compare model predictions with population sizes and dynamics seen in the field.

PLANT DEMOGRAPHY

Plant demographic parameters are given in Table 1. The hyperbolic density-dependence function provided a good description of the density response of *Echium* when fit to data from Grigulis (1999) (Fig. 3). Using the parameter estimates from Table 1 and equation 3, we found the plant population to be stable; at equilibrium the seed bank density of the plant population alone was 4300 m^{-2} and the equilibrium plant density was 168 m^{-2}. For three Australian grazed sites, before weevils were introduced, the average density of the seed bank and flowering plants was 3990 ± 920 m^{-2} and 201 ± 82 m^{-2}, respectively (Grigulis 1999; A. Sheppard, unpublished data). The model predictions fall well within the range of the field data. The final parameter we need to know, in order to calculate the average shoot biomass of *Echium* in a pasture, is the conversion coefficient from seeds to biomass, c, which is 0·025, estimated from Sheppard, Smyth & Swirepik (2001) and A. Sheppard (unpublished data). This is a constant, as *E. plantagineum* does not change its reproductive allocation pattern in response to plant size (Smyth, Sheppard & Swirepik 1997; Grigulis *et al.* 2001). Converting this plant density to biomass (where *F* is the average fecundity at 168 plants m^{-2}; Fig. 3), the model predicts a standing crop of 156 g m^{-2}, compared with an average, over 2 years, of 115 g m^{-2} found in the field (A. Sheppard, unpublished data). In these calculations we used the upper value of the seed bank decay (0·35) and a seed incorporation probability of 0·3.

WEEVIL DEMOGRAPHY

Demographic parameters for the weevil are given in Table 1. We estimated the impact of the weevil larvae on plant fecundity using experimental data. Individual
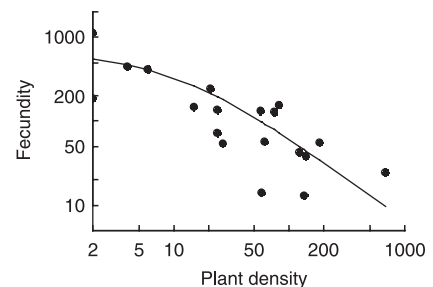
Fig. 3. Density response of *Echium* in Australian pasture. The fitted line is $F = 663/(1 + 0·1P)$, where P is plant density; $R^2 = 0·56$, $n = 19$. We fitted a more general model where the denominator was raised to the power b, but this did not significantly improve the fit of the model. Testing if $b = 1$ gave $t = 0·816$, $P > 0·4$.
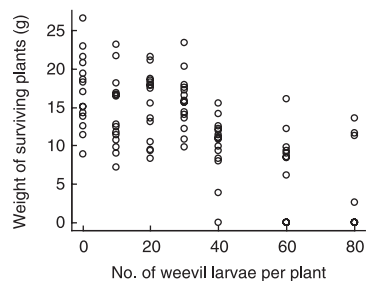
Fig. 4. *Echium* biomass as a function of the inoculum of weevil eggs placed on a plant. Open circles are the experimental data.
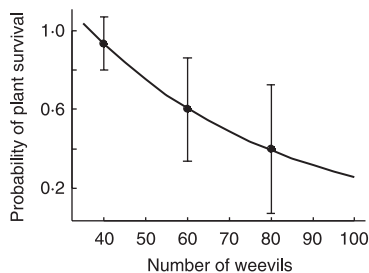

Fig. 5. The probability of plant survival as a function of the size of the inoculum of weevil eggs (eggs > 35). The fitted line is $p(\text{survive}) = p_s \exp(-\alpha W)$; parameters were estimated using non-linear modelling and a maximum likelihood function assuming binomially distributed errors (see Table 1).

plants were inoculated with 0, 10, 20, 30, 40, 60 and 80 eggs, and plant survival, shoot biomass and the number of weevils emerging were recorded at the end of the growing season. Over the range 0–30 weevils there was no detectable reduction in shoot biomass ($r^2 = 0.006$, $P > 0.1$, $n = 60$, average biomass 15.64 ± 0.56 g); similarly for surviving plants that received 40 or more weevil eggs, average shoot biomass was constant ($r^2 = 0.02$, $P > 0.1$, $n = 27$, average biomass 10.29 ± 0.59 g) (Fig. 4). Plants receiving 40 or more weevil eggs were only 66% of the size of plants receiving fewer eggs. All plants receiving less than 40 eggs survived, whereas the survivorship of those receiving 40 or more eggs decreased exponentially with the number of eggs added (Fig. 5). Combining this information on biomass reduction and plant mortality due to weevil attack, we constructed a damage function of the following form:

$$f_d = 1, E \leq 35$$
$$f_d = 0.66\, p_s \exp(-\alpha E), E > 35 \qquad \text{eqn 8}$$

where f_d gives the fraction by which average plant fecundity is reduced by the feeding of weevil larvae. To assess the effects of plant tolerance to herbivory (equation 8), we also fitted a simple exponential damage function of the form:

$$f_d = \beta_0 \exp(-\beta E) \qquad \text{eqn 9}$$

The fitted relationship assuming a herbivore tolerance damage function (equation 8) was estimated as $p_s =$
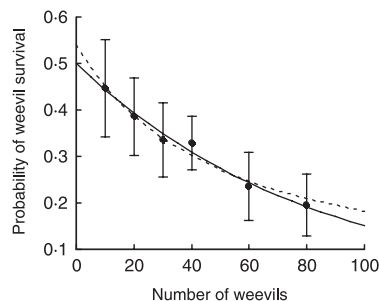
Fig. 6. Probability of a weevil successfully emerging as a function of the number of eggs used to inoculate the plant. Solid circles are the probability of emergence, the vertical lines are ± 2 SE. The solid line is the fitted function $p_s = w_s \exp(-uE)$; the dashed line is the fitted function $p_s = w_s/(1 + uE)$. The parameters were estimated using maximum likelihood, assuming the data were drawn from a binomial distribution (see Table 1).

$2.21 (\pm 0.71)$ and $\alpha = 0.0216 (\pm 0.008)$; parameters were estimated using the non-linear modelling function (nlm) in R 1·9·0 (R Development Core Team 2004), with a maximum likelihood function assuming binomially distributed errors. The fitted relationship assuming a simple exponential damage function (equation 9) was estimated as $\beta_0 = 18.2 (\pm 0.95)$ and $\beta = 0.014 (\pm 0.002)$; parameters were estimated using a generalized linear model with normally distributed errors. The simple damage function (equation 9) provided a reasonable description of the data but systematically differed from the data by predicting a continuous decline in plant size, whereas the data suggested that plants can compensate for low levels of weevil damage.

From this data set, we also estimated the density dependence acting on the weevil larvae. The probability of emergence was equally well described by both a simple exponential function (scramble competition), and an asymptotic function (contest competition) of the forms (Fig. 6):

$$p(\text{survival}) = w_s \exp(-uE) \qquad \text{eqn 10}$$

$$p(\text{survival}) = \frac{w_s}{1 + uE} \qquad \text{eqn 11}$$

where parameters were fit using maximum likelihood with binomial errors. Scramble and contest modes of competition fit the data equally well, and so both functional forms were used in numerical simulations.
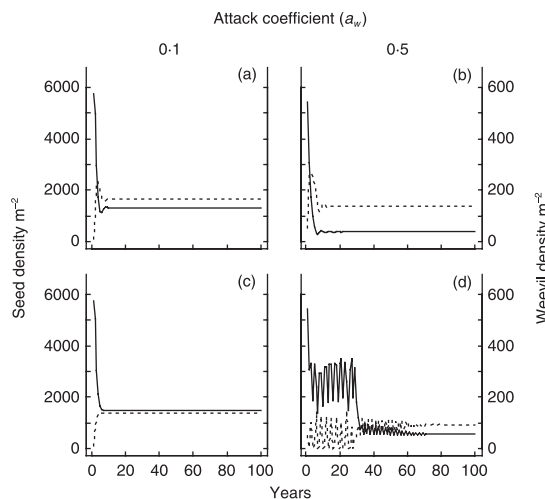
The attack coefficient, a_w, cannot be estimated directly as the number of eggs laid per weevil per plant is difficult to measure in the field. At the Yanco site, however (for a description of the methods and site see Sheppard, Smyth & Swirepik 1999), destructive sampling allowed the distribution of the number of eggs and larvae per plant to be recorded, and these were used to derive estimates of the attack coefficient. The coefficient is given by $a_w = \bar{E}_t / W_t$, where $\bar{E}_t$ is the average number of eggs laid per plant, measured by destructive harvests, and W_t is the total number of weevils at time t, giving

$a_w = \bar{E}_t/W_t = \bar{E}_t/\sum_{i=1}^{N}(E_{i,t-1}w_{s,i})$ where $w_{s,i}$ is the probability of survival of weevils in plant i and the denominator is the sum of weevils from each plant in the sampled area.

We estimated the attack coefficient, a_w, using two different methods. The first method ignored density-dependent survival and we calculated probability of larval survival, w_s, using the scramble competition model (equation 10) with the number of weevils set to one per plant. The second method used the scramble density-dependent larval survival function to predict the number of weevils emerging from the distribution of eggs laid. Because of low attack rates and therefore little evidence of density dependence in the weevil population, the attack coefficients estimated by these two methods are similar (see Appendix 2). The study area at Yanco is relatively small (50×90 m) and therefore many weevils leave the study area, leading to underestimation of the attack coefficient, particularly when weevil density is high. This results in a negative relationship between weevil population size and a_w. For this reason we consider low-density higher values of a_w ($> 0 \cdot 1$) to be more accurate estimates than lower values obtained at high weevil density (see Fig. 7 for a comparison of dynamics using values of a_w of $0 \cdot 1$ and $0 \cdot 5$). The value of a_w used determines the value of seed and weevil equilibria predicted but does not change the qualitative dynamics of the system, except at very high values of a_w (c. $0 \cdot 5$) (Fig. 7).
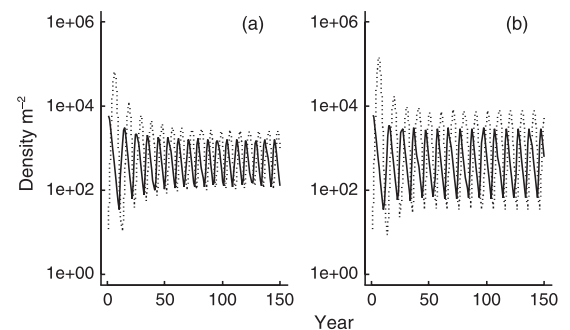
SIMULATION MODELS

It was not possible to investigate the dynamics of models incorporating both plant and weevil density dependence analytically, and we therefore used numerical simulation. Using the plant density-dependent model with a seed bank (equation 4), with density-dependent larval survival (contest or scramble competition, equations 5 and 6) and herbivore tolerance or simple damage functions (equations 8 and 9), we simulated invasion of a single pregnant weevil into a plant population at equilibrium (5819 seeds, $l = 0 \cdot 4$; all other parameters are as in Table 1). The decay coefficients in the damage and survival functions (v and u) were expressed on a per biomass basis by multiplying by the average shoot biomass of plants receiving 30 or fewer larvae. The threshold number of weevils in the herbivore tolerance damage function was determined as the number of weevil eggs/larvae per plant per unit of average shoot biomass. The results of the simulations are shown in Fig. 7. Models using the simple damage function and herbivore tolerance damage function produced similar results. For the contest competition model with the herbivore tolerance damage function, the seed bank density was 1253 m^{-2} and the weevil density was 147 m^{-2}; the shoot biomass fell from 156 g m^{-2} to 137 g m^{-2} after 100 generations. Results of the contest competition model with the simple damage function are given in Fig. 7a,b. More substantial reductions in seed bank density and biomass could be achieved with higher values of a_w. Scramble competition models behaved similarly to contest competition models at low and moderate values of a_w (Fig. 7c,d). At high values of a_w, however, scramble competition was destabilizing (Fig. 7d).

Removing density-dependent larval survival leads to oscillatory dynamics, with weevil populations achieving unrealistically high densities (Fig. 8). Use of the herbivore tolerance damage function increases both the period and amplitude of the oscillations. The reason for this is that when weevil population sizes are low, plants compensate for herbivory and so recover to high levels before the weevil population starts to recover. The resulting high density of plants allows the weevil populations to increase, leading to higher amplitude cycles than in the simple damage model. Using our estimated parameter values, if we remove plant competition from the model we find that contest competition among the weevils is not sufficient to stabilize the

Fig. 7. Model predictions for the plant and weevil density-dependent model, with a seed bank, the simple damage function and the attack coefficient $a_w = 0 \cdot 1$ or $0 \cdot 5$. The two columns correspond to the different attack coefficients; the first row is contest competition (a and b) and the second row is scramble competition (c and d). The solid line is the seed bank density; the broken line is weevil density. The herbivore tolerance function gave very similar results to the model with just a simple damage function.

Fig. 8. Model predictions for the plant density-dependent model without density-dependent larval survival and using either the exponential damage function (a) or the herbivore tolerance damage function (b). The solid line is the seed bank density; the broken line is the weevil density.

system, but scramble competition leads to stability. This can be confirmed by examining the stability diagrams in Fig. 2. For contest competition $v/u = 0.7$ and $R_{0SB} = 17.8$, which is outside the stability boundaries for $\rho = 0.57$ (critical R_{0SB} for stability *c.* 5). For scramble competition $R_{0SB} = 17.8$ at $\rho = 0.57$, which is within the stability boundary (critical R_{0SB} for stability *c.* 23).

Discussion

In this study we outlined a series of models of increasing complexity and analysed the dynamic roles of demographic processes for which there is experimental or observational evidence. Formation of a seed bank, plant and herbivore density dependence and plant compensation for low levels of herbivore attack, all have an impact on the dynamics and equilibrium densities of the plant-herbivore system. Exploring the dynamic properties of the plant–herbivore system enables us to make predictions and recommendations about the impact and sustainability of biocontrol. The aim of classical biocontrol is to introduce a control agent that will maintain the target population at a low level. By depressing the plant population to a low level, the need for repeated reintroduction should be unnecessary. Oscillations, particularly those of large amplitude, heighten the risk of stochastic extinction of the biocontrol agent. In addition, oscillations lead to periodic outbreaks of the invasive species, causing increased damage in outbreak years. Stability analysis enables us to pinpoint those aspects of the system that confer stability and predict whether the aims of classical biocontrol can be fulfilled given the parameter values and functional forms estimated from current data.

Stochasticity due to variable environmental conditions will affect many of the parameters in this model; some sites may be better or worse for weevil establishment, for example. This variability is likely to affect transient dynamics and the level of the equilibrium achieved. Our stability analysis, however, should enable assessment of whether certain parameter combinations are likely to lead to stability or not (e.g. comparing actual parameter values with Figs 1 and 2). Parameter estimates used here were collected from a number of small-scale studies; the dynamics of the system over larger scales will depend on the spatiotemporal variability of parameters and population densities and non-linearities at the local scale (Chesson 2001).

PLANT DENSITY DEPENDENCE

Density dependence in the plant population without weevil density dependence (equation 4) is stabilizing at low values of R_{0SB} but not for the values recorded for *Echium* in the field (stability conditions equations A3 and A4 are false for our estimated parameter values; see Appendix 1). Plant density dependence does, however, increase the range of starting values and parameters over which the weevil density-dependent model is

stable. It is plant density dependence that maintains biomass at a high level even when fewer plants are present, as at low densities plants are larger. This has been shown to make control difficult in other species, even in the absence of a seed bank, as large reductions in seed input are necessary in order to achieve detectable reductions in biomass (Gonzalez-Andujar 1996; Buckley *et al.* 2001).

WEEVIL DENSITY DEPENDENCE

The simplest *Echium–Mogulones* coupled model is based on a N-B host–parasitoid model but differs from it in the form of the herbivore equation, with the potential for more than one weevil to emerge from each plant. In the standard N-B host–parasitoid model only one offspring per host is produced, which is equivalent to an extreme form of contest competition (Taylor 1988). Taylor (1988) was the first to incorporate within-host competition into the N-B model, using both contest and scramble competition functions. We found weevil density dependence to be stabilizing, echoing Taylor's (1988) results for animal systems. Similar results for predator–prey and host–parasitoid models have been presented by other authors (Beddington, Free & Lawton 1975; May & Hassell 1981; May *et al.* 1981).

The choice of functional form of processes such as density dependence can have a profound effect on predictions of the dynamics and the optimal management strategy recommended (Wood & Thomas 1999; Gonzalez-Andujar & Hughes 2000; Runge & Johnson 2002). For the *Echium–Mogulones* system, the functional form of herbivore density dependence is relatively unimportant over the range of data available for parameterization; however, the functional forms differ in their stability properties. For our estimated parameters and a model without plant density dependence, scramble competition among weevils is more stable than contest competition, but the opposite is the case when plant density dependence is included in the model. At high attack rates in the model with plant density dependence and competition between weevils, the form of the weevil competition function is important for predicting the resulting dynamics (compare Fig. 7b,d).

DAMAGE FUNCTIONS

The herbivore tolerance damage function assumes that plants can compensate for low levels of weevil attack, introducing a time-lag into the system when weevil numbers are low. Time-lags are notoriously destabilizing (Crone 1997). When the system is close to instability, such as when density-dependent larval survival is removed, the herbivore tolerance damage function can lead to higher amplitude cycles than the simple damage function (Fig. 8). The strategy of tolerance to herbivory through compensatory fecundity has the ability to destabilize dynamics, but in this system the stabilizing influence of weevil density dependence compensates for the destabilizing effect of plant tolerance of herbivory.

PREDICTIONS AND RECOMMENDATIONS

Using simulation models we predict that invasion of weevils into the plant population (simulating initial release of the biocontrol agent) will result in stable coexistence between the two species, with the seed bank density of *E. plantagineum* falling to less than a third of its value without the herbivore; biomass is also decreased to about 87% of its former value. These predictions were made using a conservative estimate of the weevil attack coefficient ($0·1$ eggs plant^{-1} weevil^{-1}); higher values of a_w lead to greater reductions in seed bank density but at very high levels can cause transient instability in combination with scramble competition. For the Yanco sites, where data on weevil numbers and attack rates were collected from 1993 to 2002, the plant population was wiped out in 1998 and 2001 (Sheppard *et al.* 2002), indicating that high attack rates are possible in the field.

Our results highlight the importance of including both plant and herbivore dynamics in any weed biological control model. We have strong evidence that density dependence is important in both plant and herbivore populations. Analytical and simulation results demonstrate that density dependence, the functional form of that density dependence and its interaction with other components of the system are crucial determinants of the dynamics. *Mogulones larvatus* larvae live within the stem of their host-plant, which can lead to strong intraspecific competition for the host resources when several eggs are laid on one plant. This density dependence is crucially important for maintaining a stable interaction between the plant and herbivore. There is a 'window' of values for weevil density dependence that will lead to stable dynamics: if competition is weak, or too strong, an unstable interaction will result, leading to population cycles of plants and weevils. Characterizing the density dependence of new biocontrol agents is therefore important for predicting whether the aims of classical biocontrol (low, stable and sustainable populations of plant and herbivore) can be achieved. Further work should be done to characterize the form and strength of density dependence in biocontrol agents of different guilds or functional types, for example density dependence in stem borers (such as *M. larvatus*) might be quite different to the form and strength of density dependence in defoliators.

This is the first study to our knowledge to explore the dynamic effects of different herbivore damage functions, allowing us to quantify the effect of plant tolerance of herbivory on the population dynamics of a plant–herbivore system. Although we found that, for this system, the destabilizing effects of plant tolerance of herbivory are countered by the stabilizing influence of weevil density dependence, it should be borne in mind that in systems close to instability plant tolerance can further destabilize the dynamics. This study moves us closer to identifying those characteristics of plant and biocontrol agent populations that provide environmentally or economically acceptable control that is stable and sustainable, allowing better choices of appropriate biocontrol agents to be made.

Supplementary material

The following material is available from
http://www.blackwellpublishing.com/products/
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Appendix 1. A brief outline of the stability analysis of the models presented.

Appendix 2. Estimated attack coefficients for the Yanco data.

References

Barlow, N.D. (1999) Models in biological control: a field guide. *Theoretical Approaches to Biological Control* (eds B.A. Hawkins & H. V. Cornell), pp. 43–68. Cambridge University Press, Cambridge, UK.

Beddington, J.R., Free, C.A. & Lawton, J.H. (1975) Dynamic complexity in predator–prey models framed in difference equations. *Nature*, **255**, 58–60.

Buckley, Y.M., Hinz, H.L., Matthies, D. & Rees, M. (2001) Interactions between density-dependent processes, population dynamics and control of an invasive plant species, *Tripleurospermum perforatum* (scentless chamomile). *Ecology Letters*, **4**, 551–558.

Buckley, Y.M., Rees, M., Paynter, Q. & Lonsdale, W.M. (2004) Modelling integrated weed management of an invasive shrub in tropical Australia. *Journal of Applied Ecology*, **41**, 547–560.

Burdon, J.J., Marshall, D.R. & Brown, A.H.D. (1983) Demographic and genetic changes in populations of *Echium plantagineum*. *Journal of Ecology*, **71**, 667–678.

Caughley, G. & Lawton, J.H. (1981) Plant–herbivore systems. *Theoretical Ecology Principles and Applications* (ed. R.M. May), pp. 132–166. Blackwell Scientific Publications, Oxford, UK.

Chase, J.M., Leibold, M.A. & Simms, E. (2000) Plant tolerance and resistance in food webs: community-level predictions and evolutionary implications. *Evolutionary Ecology*, **14**, 289–314.

Chesson, P. (2001) Metapopulations. *Encyclopedia of Biodiversity, Volume 4* (ed. S.A. Levin), pp. 161–176. Academic Press, San Diego, CA.

Crawley, M.J. (1983) *Herbivory. The Dynamics of Animal–Plant Interactions*. Blackwell Scientific Publications, Oxford, UK.

Crone, E.E. (1997) Parental environmental effects and cyclical dynamics in plant populations. *American Naturalist*, **150**, 708–729.

Fernández Alés, R., Leiva, J. & Laffarga, J.M. (1991) Los pastizales del Campo de Gibraltar (Cádiz). Composición florística y calidad. *Boletín de la Real Sociedad Española de Historia Natural (Sección Biológica)*, **87**, 61–72.

Gillman, M.P. & Crawley, M.J. (1990) A comparative evaluation of models of cinnabar moth dynamics. *Oecologia*, **82**, 437–445.

Gonzalez-Andujar, J.L. (1996) High control measures cannot produce extinction in weed populations. *Ecological Modelling*, **91**, 293–294.

Gonzalez-Andujar, J.L. & Hughes, G. (2000) Complex dynamics in weed populations. *Functional Ecology*, **14**, 524–526.

Grigulis, K. (1999) *Comparative population dynamics of* Echium plantagineum *L. between its native and invasive ranges*. PhD Thesis. Australian National University, Canberra, Australia.

Grigulis, K., Sheppard, A.W., Ash, J.E. & Groves, R.H. (2001) The comparative demography of the pasture weed *Echium plantagineum* between its native and invaded ranges. *Journal of Applied Ecology*, **38**, 281–290.

Gurney, W.S.C. & Nisbet, R.M. (1998) *Ecological Dynamics*. Oxford University Press, New York, NY.

Gurney, W.S.C., McCauley, E., Nisbet, R.M. & Murdoch, W.W. (1990) The physiological ecology of *Daphnia*: a dynamic model of growth and reproduction. *Ecology*, **71**, 716–732.

Halley, J.M. & Dempster, J.P. (1996) The spatial population dynamics of insects exploiting a patchy food resource: a model study of local persistence. *Journal of Applied Ecology*, **33**, 439–454.

Hassell, M.P. (1978) *The Dynamics of Arthropod Predator–Prey Systems*. Princeton University Press, Princeton, NJ.

Juenger, T. & Lennartsson, T. (2000) Tolerance in plant ecology and evolution: toward a more unified theory of plant–herbivore interaction. Preface. *Evolutionary Ecology*, **14**, 283–287.

Lakhani, K.H. & Dempster, J.P. (1981) Cinnabar moth and its food plant, ragwort: further analysis of a simple interaction model. *Journal of Animal Ecology*, **50**, 231–249.

Lonsdale, W.M., Farrell, G. & Wilson, C.G. (1995) Biological control of a tropical weed: a population model and experiment for *Sida acuta*. *Journal of Applied Ecology*, **32**, 391–399.

McCauley, E., Nisbet, R.M., Murdoch, W.W., de Roos, A.M. & Gurney, W.S.C. (1999) Large-amplitude cycles of *Daphnia* and its algal prey in enriched environments. *Nature*, **402**, 653–656.

MacDonald, N. & Watkinson, A.R. (1981) Models of an annual plant population with a seed bank. *Journal of Theoretical Biology*, **93**, 643–653.

May, R.M. (1974) *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton, NJ.

May, R.M. & Hassell, M.P. (1981) The dynamics of multiparasitoid–host interactions. *American Naturalist*, **117**, 234–261.

May, R.M., Hassell, M.P., Anderson, R.M. & Tonkyn, D.W. (1981) Density dependence in host–parasitoid models. *Journal of Animal Ecology*, **50**, 855–865.

van der Meijden, E., Nisbet, R.M. & Crawley, M.J. (1998) The dynamics of a herbivore–plant interaction, the cinnabar moth and ragwort. *Insect Populations* (eds J.P. Dempster & I.F.G. McLean), pp. 291–308. Kluwer Academic Publishers, Dordrecht, the Netherlands.

Nicholson, A.J. & Bailey, V.A. (1935) The balance of animal populations. *Proceedings of the Zoological Society of London*, **1**, 551–598.

Nisbet, R.M., McCauley, E., de Roos, A.M., Murdoch, W.W. & Gurney, W.S.C. (1991) Population dynamics and element recycling in an aquatic plant herbivore system. *Theoretical Population Biology*, **40**, 125–147.

Noy-Meir, I. (1975) Stability of grazing systems: an application of predator–prey graphs. *Journal of Ecology*, **63**, 459–481.

Noy-Meir, I., Gutman, M. & Kaplan, Y. (1989) Responses of Mediterranean grassland plants to grazing and protection. *Journal of Ecology*, **77**, 290–310.

Piggin, C.M. & Sheppard, A.W. (1995) Echium plantagineum L. *The Biology of Australian Weeds* (eds R.H. Groves, R.C.H. Shepherd & R.G. Richardson), pp. 87–110. Richardson, Melbourne, Australia.

R Development Core Team (2004) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rees, M. & Hill, R.L. (2001) Large-scale disturbances, biological control and the dynamics of gorse populations. *Journal of Applied Ecology*, **38**, 364–377.

Rees, M. & Paynter, Q. (1997) Biological control of Scotch broom: modelling the determinants of abundance and the potential impact of introduced insect herbivores. *Journal of Applied Ecology*, **34**, 1203–1221.

Ringel, M.S., Rees, M. & Godfray, H.C.J. (1998) The evolution of diapause in a coupled host–parasitoid system. *Journal of Theoretical Biology*, **194**, 195–204.

Runge, M.C. & Johnson, F.A. (2002) The importance of functional form in optimal control solutions of problems in population dynamics. *Ecology*, **83**, 1357–1371.

Shea, K. & Kelly, D. (1998) Estimating biocontrol agent impact with matrix models: *Carduus nutans* in New Zealand. *Ecological Applications*, **8**, 824–832.

Shea, K., Smyth, M., Sheppard, A.W., Morton, R. & Chalimbaud, J. (2000) Effect of patch size and plant density of Paterson's curse (*Echium plantagineum*) on the oviposition of a specialist weevil, *Mogulones larvatus*. *Oecologia*, **124**, 615–621.

Sheppard, A.W., Rees, M., Smyth, M., Grigulis, K. & Buckley, Y.M. (2002) Modelling the population interactions between the crown weevil *Mogulones larvatus* and its host plant *Echium plantagineum*. *13th Australian Weeds Conference, 9–12 September 2002* (eds H. Spafford Jacob, J. Dodd & J.H. Moore), pp. 248–251. Plant Protection Society of Western Australia, Perth, Australia.

Sheppard, A.W., Smyth, M. & Swirepik, A. (1999) Impact of the root-crown weevil (*Mogulones larvatus*) and other biological control agents on Paterson's curse in Australia: an update. *Proceedings of the 12th Australian Weeds Conference, 2001* (eds A.C. Bishop, M. Boersma & C.D. Barnes), pp. 343–346. Tasmanian Weed Society, Devonport, Tasmania.

Sheppard, A.W., Smyth, M.J. & Swirepik, A. (2001) The impact of a root-crown weevil and pasture competition on the winter annual *Echium plantagineum*. *Journal of Applied Ecology*, **38**, 291–300.

Simberloff, D. & Stiling, P. (1996) How risky is biological control? *Ecology*, **77**, 1965–1974.

Smyth, M.J., Sheppard, A.W. & Swirepik, A. (1997) The effect of grazing on seed production in *Echium plantagineum*. *Weed Research*, **37**, 63–70.

Strauss, S.Y. & Agrawal, A.A. (1999) The ecology and evolution of plant tolerance to herbivory. *Trends in Ecology and Evolution*, **14**, 179–185.

Taylor, A.D. (1988) Parasitoid competition and the dynamics of host–parasitoid models. *American Naturalist*, **132**, 417–436.

Turchin, P. (2003) *Complex Population Dynamics. A Theoretical/Empirical Synthesis*. Princeton University Press, Princeton and Oxford.

Watkinson, A.R. (1980) Density dependence in single-species populations of plants. *Journal of Theoretical Biology*, **83**, 345–357.

Watkinson, A.R. (1990) The population dynamics of *Vulpia fasciculata*: a 9-year study. *Journal of Ecology*, **78**, 196–209.

Watkinson, A.R. & Davy, A.J. (1985) Population biology of salt-marsh and sand dune annuals. *Vegetatio*, **62**, 487–497.

Watkinson, A.R. & Lonsdale, W.M. & Andrew, M.H. (1989) Modelling the population dynamics of an annual plant *Sorghum intrans* in the wet–dry tropics. *Journal of Ecology*, **77**, 162–181.

Wood, S.N. & Thomas, M.B. (1999) Super-sensitivity to structure in biological models. *Proceedings of the Royal Society London, Series B*, **266**, 565–570.