

## Modelling the population interactions between the crown weevil *Mogulones larvatus* and its host plant *Echium plantagineum*

Andy Sheppard<sup>1</sup>, Mark Rees<sup>2</sup>, Matthew Smyth<sup>1</sup>, Karl Grigulis<sup>3</sup> and Yvonne Buckley<sup>2</sup>

<sup>1</sup>CRC for Weed Management Systems, CSIRO Entomology, GPO Box 1700, Canberra, ACT 2601, Australia

<sup>2</sup>NERC Centre for Population Biology, Imperial College, Silwood Park, Ascot, Berks SL5 7PY, UK

<sup>3</sup>NSW Agriculture, c/o CSIRO, GPO Box 1600, Canberra, ACT 2601, Australia

**Summary** A biological control program against Paterson's curse, *Echium plantagineum*, in Australian pastures has been underway since the late 1970s. The most successful biological control agent to date has been the root-crown weevil *Mogulones larvatus*. This paper conceptually presents a population model for the interactions between *E. plantagineum* and the crown weevil based on field collected ecological data. We show how this model can be used to predict the impacts of biological control of the weevil on this weed. We also illustrate that increasing complexity in the model appears to indicate that over-simple ecological models of weed biological control systems may over-estimate long-term impacts on the target weed. Impact predictions are presented of the likely long-term reductions of Paterson's curse that we expect to see in the field, and show that these predictions are at least reasonably reliable when compared to field impacts recorded so far. **Keywords** Biological control, weeds, Boraginaceae, Curculionidae, population biology, ecological modelling.

### INTRODUCTION

The frequently quoted benefits of using biological weed control are that this form of weed management is both target-specific and largely environmentally benign, if not beneficial, through reduced herbicide usage. It is also perhaps the only form of weed management where weed abundance is permanently reduced (Briese 2000). Biological control is risky however, with a low success rate (more than half the attempts fail to have any impact), and has potential negative off-target impacts. It also may take a long time (tens of years) to reach full impact and fails, by itself to address weed replacement problems. The CRC for Australian Weed Management is making advances in the science behind biological control in order to improve success rate and reduce the time to impact of biological control agents. The CRC hopes to achieve this by improving biocontrol agent selection, risk assessment protocols, release strategies and redistribution networks and incorporating biological control into integrated management strategies that will better weed-proof ecosystems.

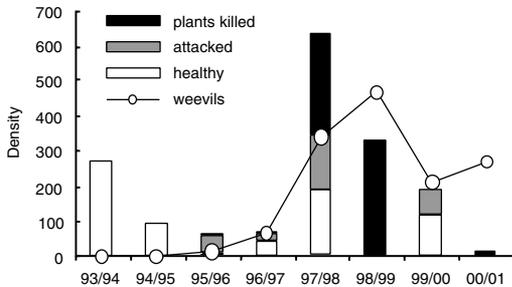
Biological control has a long tradition of using ecological models to untangle interactions between biological control agents and their hosts to help understand how such agents either fail or succeed in suppressing their hosts. Such models can also be used to allow prediction of impacts and benefits across the large timeframes between initial release and maximum impact across wide geographic areas. In host-parasitoid systems these models have achieved some complexity providing detailed evidence of some subtle stabilising mechanisms in the interactions between populations of agent and target (Murdoch and Briggs 1996). Such models in weed biological control have, in general, been quite simple by comparison. In most cases the models used have been based on the dynamics of the host plant incorporating the impact of the insect herbivore as a constant or stochastic variable within a range defined from field observation. Such modelled systems either incorporate no internal population regulation or are regulated by density dependence of the weed population only.

In this paper we present an ecological population model of the interactions between a root-crown boring weevil, *Mogulones larvatus*, introduced into Australia and locally wiping out populations of the annual pasture weed, *Echium plantagineum*. First we present a simple weed-weevil model of the population dynamics of *E. plantagineum* with density dependent fecundity and which, like others in the past, incorporates weevils effects as a constant reduction in survival and/or fecundity of the host plant. We then present a more complex model incorporating the population dynamics of the weevil in addition to that of its weed host in which density dependence is present in both weevil and host plant components of this model.

The aims of this paper are then to briefly explore how the interaction between *E. plantagineum* and *M. larvatus* is affected by a) the presence of weed seed-bank, b) density dependence in both weed and weevil, and c) to predict the long-term success of biological control of *E. plantagineum* with this insect.

WEEVIL-PLANT SYSTEM IN THE FIELD

*Echium plantagineum* is a winter annual which forms a persistent seed bank. *Mogulones larvatus* has now established at 35% of over 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. At one site in particular, Yanco (southern NSW), where data on weevil numbers and attack rates were collected from 1993 to 2001 the weevil population has regularly killed the whole population of its host over 1.5 ha preventing any seed production. In 1998 the new-generation weevils emerged from this site at a density of 446 m<sup>-2</sup> (Figure 1, Sheppard *et al.* 1999).



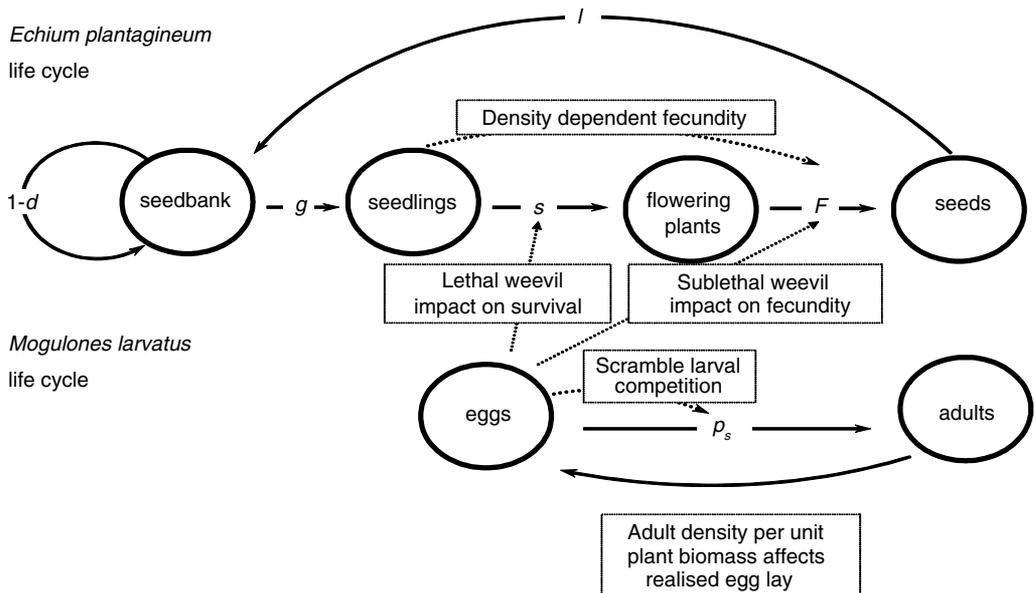
**Figure 1.** Field densities of healthy and dead *E. plantagineum* and the weevils that attacked them at Yanco site NSW.

In a field impact experiment set up in Canberra (Australia) in 1994 and repeated using the resident weevil population in 1995, *M. larvatus* reduced seed production of attacked plants by 16% and 72%. (Sheppard *et al.* 2001).

Parameter estimates for the models came from previous fieldwork on the ecology of *Echium plantagineum* and unpublished data (e.g. Grigulis *et al.* 2001). One control temperature room experiment provided additional impact functions. In this experiment equal sized individual plants were inoculated with 0, 10, 20, 30, 40, 60 and 80 weevil 1st instar larvae. Plant biomass at the end of the growing season and the number of weevils emerging was recorded. The resulting data from this experiment (not shown) were used to generate functions for the effect of weevil number on plant survival (lethal effects) and fecundity of survivors (sublethal effects) and the relationship between larval density and adult emergence (see below).

LIFE CYCLES AND MODEL DESCRIPTIONS

In this section we present a conceptual overview of the model's design. The mathematical equations will appear in a theoretical paper in preparation. Both *E. plantagineum* and *M. larvatus* have annual lifecycles (Figure 2). *Echium* seeds germinate and establish from the seedbank in autumn with *g* germination/establishment probability (0.13 Grigulis *et al.* 2001). The rest of the seedbank has a field estimated 1-*d* (*d* = 0.65, Grigulis *et al.* 2001) chance of surviving to the



**Figure 2.** Model structure.

following year. Weevil adults emerge from over-summering in autumn and start laying eggs on established *Echium* rosettes. The number of eggs successfully laid per plant per unit area depends on the ratio between weevil density observed in the field (Figure 3).

Low laying rates per weevil effectively leads to density dependent emigration out of the weed population (weevil spread). The survival probability of *Echium* plants to maturity,  $s$  was both field estimated without weevils (0.3, Grigulis *et al.* 2001) and augmented by multiplying plant number by  $2.21 \exp(-0.02 \text{eggs})$ , an experimentally generated relationship between weevil number and plant survival for plants if the number of weevil eggs laid per plant was  $>35$  (lethal effects). *Echium* plants grow towards a predictable final field estimated maximum average biomass per mature plant in spring of 12.1 g (field estimated). They are prevented from achieving this size by a density dependent function driven by seedling density, where maximum average biomass is divided by  $1+0.1 \cdot \text{plant density}$  (Watkinson 1980). The biomass of *Echium* plants at maturity is also reduced by multiplying with a function  $\exp(-0.014 \text{eggs})$  (M. Smyth and A. Sheppard unpublished experimental data) dependent on the number of weevil eggs laid per plant (sublethal effects). Seed production,  $F$  is a function of mature plant biomass (55 seeds  $\text{g}^{-1}$ , Smyth *et al.* 1997, Grigulis *et al.* 2001). The seeds enter the seedbank at a field estimated seedbank incorporation rate,  $l$  of 0.4 (Grigulis *et al.* 2001). Weevils can also undergo density dependent contest competition reducing their survival; the probability of surviving per plant  $p_s$  being dependent on the experimentally generated relationship where  $p_s = 0.5 \exp(-0.012 \text{eggs})$ .

RESULTS

Running the model with only density dependence in the plant and without the weevils gave an equilibrium seed bank density  $\approx 3800$  seeds  $\text{m}^{-2}$  and the equilibrium plant density  $\approx 150$   $\text{m}^{-2}$ . This compared favourably with the average field density of the seed bank  $3990 \pm 920$   $\text{m}^{-2}$  and flowering plants  $201 \pm 82$   $\text{m}^{-2}$  recorded at Australian sites (Grigulis *et al.* 2001, A. Sheppard unpublished). The model predicts a standing crop of  $\approx 110$   $\text{g m}^{-2}$ , compared with an average field estimate over two years, of 115  $\text{g m}^{-2}$  (Grigulis *et al.* 2001). Removing the seedbank by preventing the carryover of seed in the soil from one year to the next made the conditions for stability more stringent, decreasing the range of parameter values where a stable equilibrium density could be reached.

The plant model was expanded to incorporate invasion by the weevil into the plant population at this equilibrium. The density dependent plant model was

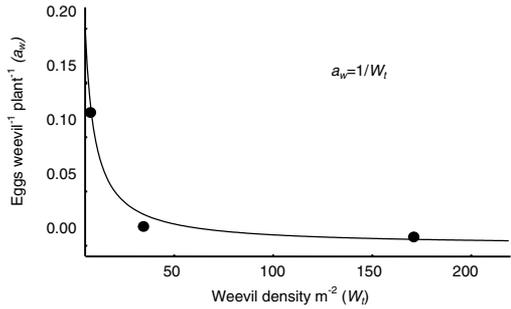


Figure 3. Change in weevil attack rate with weevil density.

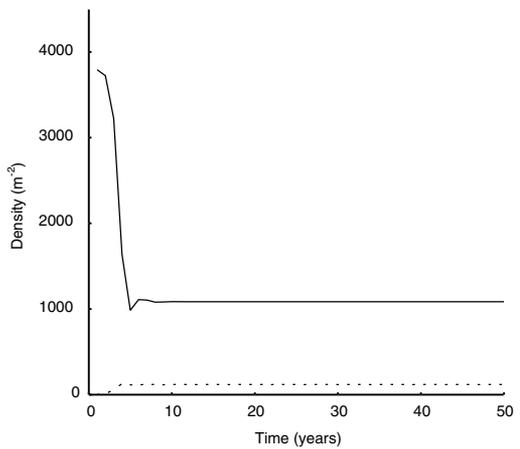
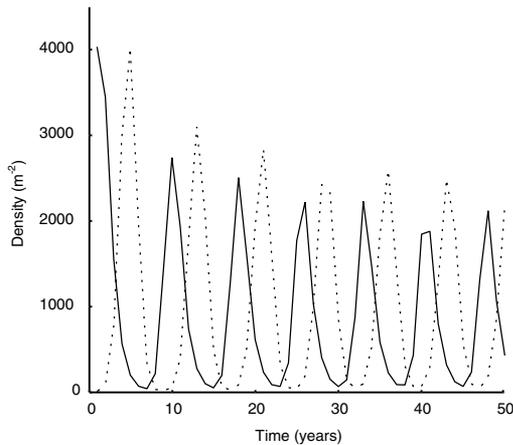


Figure 4. Model predicted change in *Echium* seedbank density (solid line) following introduction of the weevil including density dependence in the weed and the weevil. Dotted line is weevil density at equilibrium.

coupled with a weevil model with density dependent larval survival. The model predicted a stable equilibrium seedbank of  $\approx 1000$  seeds  $\text{m}^{-2}$  and a weevil density of  $\approx 120$   $\text{m}^{-2}$ ; the plant biomass fell from  $\approx 110$   $\text{g m}^{-2}$  to  $\approx 30$   $\text{g m}^{-2}$  (Figure 4). Removing density dependent larval survival in the weevil led to unstable oscillatory dynamics of weed and weevil populations with the weevils reaching unrealistically high numbers (Figure 5).

DISCUSSION

Our model for the *E. plantagineum* – *M. larvatus* system successfully estimates realistic field densities of plants, seedbank levels and mean plant weight for Australian conditions. The model, including weevil



**Figure 5.** Model predicted change in *Echium* seed-bank density (solid line) following introduction of the weevil including density dependence *only* in the weed. Dotted line is weevil density at equilibrium.

population dynamics in the model predicts a  $\approx 70\%$  reduction in mean plant and seedbank density and standing plant biomass. These predictions fit reasonably well with field observations following release at Yanco (Figure 1). Inclusion of the weevil impact as a simple constant reduction in plant fecundity generated much greater predicted impacts.

Outputs from this model highlight the following conclusions. Firstly, including a seedbank-refuge in the model increased host-plant population stability in the face of impact from the weevil. Secondly, including the weevil dynamics rather than a constant impact of attack gave less optimistic but perhaps more realistic estimates of weed reduction. Finally, density dependence in the both the weevil and host plant populations in the model increased the stability of the interactions between them. This study shows that it is valuable to move beyond simple population models for understanding the interactions between insect herbivores and their host plants, but it is vital in this process that

field data on herbivore impact be collected to ensure model output reflects damage observed in the field. In this case the comparison was good and the likelihood of a successful biological control project against Paterson's curse remains high.

#### ACKNOWLEDGMENTS

Anthony Swirepik and John Lester for help collecting data. Darren Kriticos and Art Diggle for comments on the manuscript.

#### REFERENCES

- Briese, D.T. (2000). Classical biological control. In 'Australian Weed Management Systems' ed. B.M. Sindel, pp.161-192. (R.G. and F.J. Richardson, Melbourne).
- Grigulis, K., Sheppard, A.W., Ash, J.E. and 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.
- Murdoch, W.W. and Briggs, C.J. (1996). Theory for biological control: recent developments. *Ecology* 77, 2001-2013.
- Sheppard, A.W., Smyth, M. and Swirepik, A. (2001). The impact of *Mogulones larvatus* and pasture competition on *Echium plantagineum*. *Journal of Applied Ecology* 3, 291-300.
- Smyth, M.J., Sheppard, A.W. and Swirepik, A. (1997). The effect of grazing on seed production in *Echium plantagineum* L. *Weed Research* 37, 63-70.
- Sheppard, A.W., Smyth, M.J. and 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, eds A.C. Bishop, M. Boersma, and C.D. Barnes, pp. 343-346. (Tasmanian Weed Society, Devonport).
- Watkinson, A.R. (1980). Density-dependence in single species populations of plants. *Journal of Theoretical Biology* 83, 345-357.