Modelling the population interactions between the crown weevil <i>Mogulones larvatus</i> and its host plant <i>Echium plantagineum</i>

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Summary A biological control program against Paterson's curse, <i>Echium plantagineum</i>, in Australian pastures has been underway since the late 1970s. The most successful biological control agent to date has been the root-crown weevil <i>Mogulones larvatus</i>. This paper conceptually presents a population model for the interactions between <i>E. plantagineum</i> 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, <i>Mogulones larvatus</i>, introduced into Australia and locally wiping out populations of the annual pasture weed, <i>Echium plantagineum</i>. First we present a simple weed-weevil model of the population dynamics of <i>E. plantagineum</i> 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 <i>E. plantagineum</i> and <i>M. larvatus</i> is affected by a) the presence of weed seedbank, b) density dependence in both weed and weevil, and c) to predict the long-term success of biological control of <i>E. plantagineum</i> 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⁻² (Figure 1, Sheppard et al. 1999).

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

Figure 2. Model structure.
following year. Weevil adults emerge from over-sum-
mering 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 esti-
mated 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 (le-
thal 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 \( 1+0.1\times \) 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. Shep-
lard unpublished experimental data) dependent on the
number of weevil eggs laid per plant (sublethal effects).
Seed production, \( F \) is a function of mature plant bio-
mass (55 seeds 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 prob-
ability 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 \( \approx 3800 \text{ seeds m}^{-2} \) and the equilibrium
plant density \( \approx 150 \text{ m}^{-2} \). This compared favourably with
the average field density of the seed bank 3990 ± 920
m\(^{-2}\) and flowering plants 201 ± 82 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 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 in-
vasion by the weevil into the plant population at this
equilibrium. The density dependent plant model was
coupled with a weevil model with density dependent
larval survival. The model predicted a stable equilib-
rium seedbank of \( \approx 1000 \text{ seeds m}^{-2} \) 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 oscilla-
tory 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
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.

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REFERENCES


