Ecological Principles of Biological Control: 
From Population Theory to Weed Biocontrol Practice

R. De CLERCK-FLOATE and R. S. BOURCHIER 

Agriculture and Agri-Food Canada, Lethbridge Research Centre, P.O. Box 3000, Lethbridge, Alberta, T1J, 4B1, Canada

Classical biological control of weeds is currently undergoing a critical period of self-examination that is being driven by an ecological perspective. Weed biocontrol has always been governed by ecological principles, because the tools and targets of the trade are living organisms. Despite many years of testing and releasing agents, however, there is still a need for predictive capability to describe what our agents will do in their new environments. One potential method to improve predictability is to apply existing ecological approaches and theory to operational weed biocontrol programs. As examples, we must develop ecologically-based criteria for activities such as the assessment of host range and, the creation of outbreaks of biocontrol agents for weed control. The speakers in this session have worked in a variety of ecological systems to address and test current theory in population ecology. They were asked to consider how the approaches they are using to understand insect or plant population dynamics could be used to improve the success and safety of weed biocontrol.

In addition, speakers were asked to provide a short list of “rules-of-thumb” which were the take home messages for consideration by weed biocontrol practitioners and researchers (Appendix 1). Rather than providing general answers to apply to specific projects, the rules-of-thumb are a starting point for research. They provide a list of testable hypotheses, which must be addressed through experimentation within each of our potentially unique insect-weed systems.

Population ecology provides the key underlying concepts for classical weed biocontrol, which can be defined as the manipulation of both natural enemy and host-plant numbers. Ultimately, we want to release the biocontrol agents in such a manner that an agent “outbreak” is produced, which will reduce the density of the targeted weed to an acceptable threshold level, while not damaging populations of non-target species. Several speakers addressed current hypotheses explaining how and why insect outbreaks occur, based on what is known about pest species (e.g., forest tent caterpillar; Jens Roland) and natural insect-plant systems (e.g., arroyo willow-galling sawfly system, Peter Price; goldenrod-insect herbivore system, Naomi Cappuccino). The rules-of-thumb generated from these talks deal with how to induce outbreaks by first identifying and then working with, the ecological parameters of each system. Price hypothesizes that most weed biocontrol agents are non-out-breaking species by nature and are constrained in population growth by their requirement for plants of high quality/vigor. Thus if a biocontrol insect is found to fit the “latent” population dynamics criteria described by Price, a potential application would be the manipulation of weed populations to somehow increase plant quality, thereby causing local outbreaks of the biocontrol insect. This view contrasts with one of the most commonly suggested hypotheses for the success of biological control agents: the agents do well because of the removal of the top down regulation imposed by natural enemies in the agent’s native habitat. Consideration of the host plant will provide additional...
Lessons learned from Roland’s spatially explicit studies of forest tent caterpillar populations suggest that there may be a threshold weed patch size or proximity of patches that are required for an biocontrol agent to outbreak. Determining the appropriate patch size for insect release requires studies at different spatial scales and determining the dispersal distance of the insect. From the papers of Price, Roland and Cappuccino, it is obvious that we need to be conducting ecological studies of the biocontrol agents early in programs, in both their native and new habitats, in order to understand the basic population traits that may help us in the successful application of biocontrol. As Peter McEvoy argues, before we even can ask the simple question of what is the optimum number of insects to release at a site, we must have good quantitative estimates of factors affecting the establishment, population growth or local extinction and spread of the species involved.

A critical aspect of weed biocontrol that is highlighted by both Judy Myers and Svata Louda is the need for ecologically-based studies of the impact of biocontrol agents; both on the target plants (Myers) and on non-target plants (Louda). Both authors challenge weed biocontrol researchers to be prepared for the ecological consequences of creating insect outbreaks through careful study of our systems. Myers’s hypothesis, based on population models of knapweed, is that seed-feeding insects even if in outbreak condition, may have no effect on weed populations because of the population traits of the host plant. Thus before releasing another exotic agent because it has been screened and deemed safe, we must responsibly consider its usefulness through studies of the population dynamics of the target weed. Svata Louda focuses on non-target host plants and documents an example where the successful outbreak of a biocontrol agent has had negative consequences for some non-target species. Consideration of non-target organisms has always been an issue in weed biological control and its importance will only increase.

The protection of native species should be a goal, but not a permanent barrier to the release of biocontrol agents, because invasive weeds also threaten native species. In some cases where serious effects of invasive plants on native flora and fauna can be clearly documented, we may not have time to identify all potential interactions and impacts of a potential agent before we need to act and approve a release. For all biocontrol releases, but especially for these agents, long-term impact and population studies similar to the model used by Louda are critical, so that there is improvement of biocontrol methods and pre-release predictions can be tested.

Higher rates of establishment, increased impact and better predictability are the potential gains from linking ecological theory and methods to biological control. Perhaps even more important, however, for the future of weed biocontrol is the incorporation of ecological data into a framework for decision making about biological control. We need ecological data on both sides of a release decision; what impacts are weeds having on native communities and what are potential target and non-target impacts of the biocontrol agent. Placing these data in a risk-assessment framework will allow comparisons of the impacts of all pest-control options on an equivalent scale, including the status quo. This will help provide maximal protection of non-target species and ensure that we do not abandon biological control as a strategy without careful consideration of the alternatives.
Appendix 1: Rules of Thumb

Effects of Food Resource Quality on Insect Herbivores Relevant to Weed Biocontrol: Bottoms up!

*Peter Price*

1. Bottom-up regulation of insect herbivore populations through plant quality is more prevalent than top-down regulation from carnivores - of direct importance to biocontrol attempts.

2. Host plants have dramatic impact on herbivore populations with plant architecture, age and module vigor as critical factors. Thus, management of plant quality in biocontrol can be basic for success.

3. The most favorable plant hosts for herbivores, in relation to species or quality within species, reduce the impact of carnivores on herbivorous biocontrol agents. This improves the probability of success in biocontrol.

Plant Life History, Ecology and Environment: Three Constraints on Biological Control Success

*Judy Myers*

1. Consider ability of plants to compensate for insect attack.

2. Matrix models of plant populations without density dependence may not provide realistic predictions of biological control outcomes.

3. Seed predators should not be introduced just because they have been screened.

Patch Size, Herbivore Dispersal, and Spatial Scale: Landscape Effects Promoting Herbivore Outbreak

*Jens Roland*

1. There may be a threshold amount of habitat (or size of habitat patch) needed for insect populations to reach defoliation density.

2. The threshold size may not be detectable at all spatial scales.

3. Measuring the amount of suitable habitat (or habitat ‘patch’ size) should therefore, be done at multiple spatial scales.

4. The scale at which this threshold is evident is a function of the scale of insect dispersal, and the degree of fragmentation of the habitat.

Predicting Indirect Ecological Effects: Evidence from *Rhinocyllus conicus.*

*Svata Louda*

Four “rules of thumb” that emerge from the *Rhinocyllus* case history revolve around the clear need to use ecological concepts and data to evaluate and predict non-target ecological effects:

1. Identify potentially vulnerable nontarget species within the array of phylogenetically-related ones by using ecological criteria and traits, such as phenology, life history, and morphology.

2. Believe the data from standardized feeding, oviposition and preference-performance tests, and if potential nontarget feeding is found, study possible consequences further.

3. Expect, and so measure, demographic responses to augmentation of the host plant
feeding guild on potentially vulnerable nontarget species, including determination of limiting factors.

4. If populations of potential nontarget species are limited by consumers under normal life history conditions, then the potential for significant ecological effects is high, based on the evidence from this case history.

Oviposition behavior of insects used in the biological control of weeds

Naomi Cappuccino

Insect herbivores that are considered to be pest or outbreak species tend to lay their eggs in clusters or masses, whereas non-outbreak species tend to scatter eggs singly throughout the habitat. Do successful weed biocontrol agents share this tendency to lay eggs in clusters? A survey of 39 control agents that are available from governmental agencies or commercial suppliers reveals that this is not the case; successful control agents are no more likely than randomly chosen insects to lay eggs in clusters.

Weed Biocontrol as an Invasion Process

Peter McEvoy, F. S. Grevstad, S. Schooler, M. Schat, and E. M. Coombs

1. When releasing control organisms, don’t put all your eggs in one basket. How to balance the inherent tradeoff between the size of each release and the number of releases (given a finite initial release stock) depends on the susceptibility of the particular species to factors that put small populations at risk of extinction. These factors include demographic stochasticity, environmental variability, and Allee effects (reduced population growth at low density). Demographic stochasticity is unlikely to be important for release sizes commonly used. If Allee effects are intense, favor a few, large releases. If environmental stochasticity predominates, favor many, small releases.

2. Don’t forget to FLOSS. If at first you don’t succeed, try, try again*but with a different strategy along the continuum between a Few Large or Several Small releases (the so-called FLOSS tradeoff). If establishment fails in one year, try again in another year.

3. When releasing control organisms, practice good husbandry. Transport insects promptly to a suitable field location in a stage that tolerates handling. Make releases close to home so that you can monitor them frequently. Space releases at intervals that reflect the capacity of dispersal to fill in the gaps. When Allee effects are present, release insects under cages with ample resources if this does not inhibit the capacity of control organisms to escape from adversity. Space releases of different control organisms to evaluate them separately before evaluating them jointly.

4. Don’t place too much faith on rules of thumb or you will end being all thumbs!