ATTRIBUTES OF BIOLOGICAL CONTROL AGENTS AGAINST ARTHROPODS: WHAT ARE WE LOOKING FOR?

P.G. Mason[1], P. De Clercq[2], G.E. Heimpel[3], & M. Kenis[4]

[1]Agriculture and Agri-Food Canada, Research Centre, 960 Carling Avenue, Ottawa, Ontario, Canada, masonp@agr.g.c.ca; [2]Department of Crop Protection, Faculty of Bioscience Engineering, Ghent University, Coupure Links 653, Ghent, Belgium, patrick.declercq@ugent.be; [3]Department of Entomology, University of Minnesota, 1980 Folwell Ave. St. Paul, Minnesota, U.S.A., heimp001@tc.umn.edu; [4] CABI Europe-Switzerland, 1, rue des Grillons, Delémont, Switzerland, m.kenis@cabi.org

ABSTRACT.

Biological control of arthropods is undergoing dramatic change due to heightened awareness of non-target impacts and increasing scrutiny by regulatory agencies. While global trade has contributed to a greater demand for biological control, project funding has remained stagnant or even declined. Thus, to ensure that biological control remains an important option for regulating pests there is a need to provide guidance on what agents are appropriate in a modern, science-based context. Through retrospective analysis it is clear that there are situations where arthropod biological control agents have been successful and other situations where agents failed to have an impact on target pest species, and yet other situations in which biological control agents have backfired, causing more harm than good. By determining those attributes that are associated with effective yet environmentally-benign agents, we may be able to develop recommendations that would be useful for decision-making when selecting biological control agents for study. In contrast, by determining those attributes that are associated with ineffective or environmentally damaging agents, guiding principles can be developed to facilitate avoidance of species with these characteristics.

INTRODUCTION.

Biological control of arthropod pests is an important component of cost-effective, environmentally-benign integrated pest management. Early successes in biological control were dramatic, as exemplified by the vedalia beetle suppression of cottony cushion scale, and resulted in the establishment of programs and infrastructure that focused almost exclusively on foreign exploration for new agents. Generally, if an arthropod biological control agent did not cause damage to economically-important species and no concern was raised about impacts on other non-target species it was considered appropriate for release (Greathead 1986). However, as Greathead (1986) predicted, it is now a requirement that arthropod biological control agents be screened, and assessments of potential environmental impacts be made before release can be approved for use in both augmentative and classical biological control. Science-based, regionally-harmonized regulation of introduction of exotic natural enemies has become necessary to ensure that biological control remains a viable option for managing pests (Hunt *et al.* 2008). With the increasing costs associated with research, there is an urgent challenge to develop methods and new guidelines to fulfill these regulatory requirements. Van

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Driesche & Reardon (2004) and Bigler *et al.* (2006) proposed methods for evaluating environmental impacts of biological control agents. There have been a few attempts to define what makes a good biological control agent of arthropod pests (e.g. Beddington *et al.* 1978; Kimberling 2004) and also what attributes contribute to non-target risks (Holt & Hochberg 2001; Kimberling 2004; Pearson & Callaway 2005). In addition, general principles have been proposed for predicting effectiveness of potential biological control agents. Murdoch (1994) articulated perhaps the most over-arching principle hypothesized to govern effectiveness of specialized biological control agents: agents that are able to persist at the lowest equilibrium of their prey or host should be the most effective. In addition, a number of authors have analyzed the historical record of biological control in order to identify factors or traits that are associated with success and failure (e.g. Hawkins *et al.* 1993; Hawkins & Cornell 1994; Stiling 1993, Stiling & Cornelissen 2005; Kimberling 2004). Despite these advances, there is still much room for improving in our ability to predict whether a biological control agent will succeed, fail or back fire. In this review, we provide a brief outline of some of the main issues that are the subject of the most current inquiry as an introduction to more specialized papers that follow in this session (Berkvens *et al.* 2009; Haye *et al.* 2009; Murray *et al.* 2009; Teulon *et al.* 2009).

CHARACTERIZING ATTRIBUTES OF SUCCESSFUL AGENTS.

Early summaries of biological control projects (e.g., DeBach 1974; Caltagirone 1981; DeBach & Rosen 1991; Stiling 1993) have provided insight into factors that contributed to success or failure of releases, but most do not mention what characteristics of the agents contribute to that success. Databases (e.g. Greathead & Greathead 1992) have compiled information on releases of biocontrol agents in formats that could enable the generation of statistics on successes and failures in control and these have recently been used to assess non-target impacts (e.g. Stiling & Simberloff 2000; Lynch *et al.* 2001). However, databases must be used cautiously since not all agents are thoroughly evaluated (Waage 1990). Mathematical models have been used to generate hypotheses about what attributes are associated with successful biological control agents (reviewed by Mills & Getz 1996; Murdoch *et al.* 2003; Elkinton 2008). However, relatively few empirical case studies have been used to test assumptions and predictions of these models (e.g. Hassell 1980; Godfray & Waage 1991; Murdoch *et al.* 1996). In addition, for many successful biological control projects, the general reasons for success seem relatively obvious and have been inferred empirically (Table 1).

Depending on whether an agent is intended for classical or inundative biological control the optimal state of characteristics may vary. For example, the self-perpetuation of a classical agent may require that it is able to survive extreme climate (overwinter in cold climates or aestivate in hot, dry climates) whereas agents used to overwhelm a pest in the short term (such as in glasshouse environments) may not be expected to survive extreme climates. Therefore, the optimized state may vary according to intended use. In Table 2 we have noted attributes of natural enemies predicting effectiveness that we suspect differ between classical and augmentative biological control.

Table 1. Examples of successful biological control projects and the likely reasons for their success.

Target species	Natural enemy	Likely reasons
Icerya purchasi Maskell	*Rodolia cardinalis* (Mulsant)	Thermal tolerance, short development time with respect to prey (DeBach & Quezada 1973)
Trialeurodes vaporariorum (Westwood)	*Encarsia formosa* Gahan	High dispersal ability, high searching ability, accepts all immature host stages, ease of mass rearing, (van Lenteren 1995; Hoddle *et al.* 1998)
Tetranychus urticae Koch	*Phytoseiulus persimilis* Athias- Henriot	Voracious feeding, high dispersal ability, high searching ability, ease of mass rearing, availability of pesticide-resistant strain (van Lenteren 1995)
Phenacoccus manihoti Matile-Ferrero	*Apoanagyrus lopezi* De Santis	Attack of early host instars, production of more females on young hosts, superior competitive ability, high search capacity (Neuenschwander 2001)
Aonidiella aurantii (Maskell)	*Aphytis melinus* DeBach	Thermal tolerance, ability to produce female offspring on relatively small scale insects (Luck 1986; Murdoch *et al.* 1996)

Table 2. Examples of attributes predicting success of agents differently for classical and augmentative biological control.

	Classical	Augmentative
Distribution in host native range/habitats	widespread	not required
Efficacy in native range	high	not required
Dispersal capability	high	short range important
Life cycle	synchronized with host	synchronization less important for inundative agents
Host specificity	high	high or low

There is no ideal set of attributes that guarantees success and some good attributes may not be associated with the best agents. For example, ease of rearing in culture is a practical aspect that has implications for early control of the target (Doutt & Debach 1964) and more recently for host range assessment. However this must be carefully considered because effective agents might be eliminated from further consideration solely because they are not easily reared (Waage 1990).

Phenotypic variability is an example of an attribute where the perceived optimum state can have both good and bad effects. In terms of climate matching, a high level of variation of a biological control agent (i.e. populations from as many areas as possible in the area of origin) is desirable to ensure that one of the populations matches that of the area of intended introduction. However, high genetic variability may also increase the risk of non-target impacts (Phillips *et al.* 2008).

CHARACTERIZING ATTRIBUTES OF ENVIRONMENTALLY-RISKY BIOLOGICAL CONTROL AGENTS.

Whereas it is usually rather straightforward to assess whether a biological agent has become established in nature and, subsequently, has achieved an economic impact or not, it is much more problematic to assess its non-target impact on native biodiversity and ecosystems. Among the hundreds of biological control agents established worldwide, many have been found on non-target hosts or prey (Lynch *et al.*, 2001; Kimberling 2004). Kimberling (2004) tried to use this information to detect traits associated with non-target effects. She concluded that traits that could be used to predict non-target effects included sex-ratio of progeny (female biased sex ratio being associated with lower non-target effects) and the presence of native natural enemies. However, she defined "non-target effects" as evidence from the literature that an exotic agent attacks non-target native host/prey or competes with native natural enemies. But the fact that a parasitoid or a predator is found parasitizing or feeding on a non-target species does not necessarily mean that it has a significant effect on populations of the non-target species. In their extensive literature survey on the ecological effects of alien insects, Kenis *et al.* (2009) found evidence for a significant effect on native species populations in only six intentionally introduced parasitoids and two intentionally-introduced predators (Table 3). All parasitoids and predators for which a severe non-target effect has been ascertained are known to attack a high number of hosts or prey. Thus, the rather recent move towards the selection of highly specific agents in classical biological control of arthropods is a good one (Van Driesche & Reardon 2004). Interestingly, several of the parasitoids and predators that have had documented negative effects on non-target species have also been considered "successful" agents. The tachinid *Bessa remota* (Aldrich) (Diptera: Tachinidae) has even been considered as extremely successful because it is the only parasitoid, which, in the 1920s in Fiji, is suspected to have eradicated both its target host, the coconut moth, *Levuana irridescens* Bethune-Baker (Lepidoptera: Zygaenidae) and a non-target native moth, *Herothopan dolens* Druce (Lepidoptera: Zygaenidae) (Kuris 2003). However, Kuris (2003) and Hoddle (2006) have suggested that *L. irredescens* may have survived on other islands, and also that there is little evidence *H. dolens* actually went extinct. This suggests again that traits associated with failure in control and non-target effects have to be analysed separately.

WHAT ARE WE LOOKING FOR?

There is a general consensus that no biological control agent possesses all ideal states of desirable attributes. Selection criteria based on the notion that ideal agents can be 'built' by combining desirable life-history attributes are likely wrong, due to the likelihood of correlated life-history tradeoffs, and a more realistic approach would be to focus on combinations of attributes that characterize real species (Waage 1990). Furthermore, characteristics associated with biological control agents that carry environmental risks are different from those associated with 'good' or 'failed' agents. As stated by Turnbull & Chant (1961), "… we must know much about the attributes that make an organism effective in limiting the abundance of others, how this effect is modified by undesirable characters, the mechanics of interactions, and, of course, the way in which the introduced species will fit into its new environment and its chances of survival there, and the attributes that determine this."

Table 3. Alien biological control agents for which an effect has been measured on native species populations or communities (from Kenis *et al.* 2009).

Species	Mechanism involved in the effect
Parasitoids	
Aphidius ervi (Haliday) (Hym.: Braconidae)	Parasitism
Bessa remota (Aldrich) (Diptera: Tachinidae)	Parasitism
Cales noaki Howard (Hymenoptera: Aphelinidae)	Competition with native parasitoid
Compsilura concinnata (Meigen) (Diptera: Tachinidae)	Parasitism and competition
Lisiphlebus testaceipes (Cresson) (Hymenoptera: Braconidae)	Competition with native parasitoids
Torymus sinensis Kamijo (Hymenoptera: Torymidae)	Hybridization with native parasitoid
Predators	
Coccinella septempunctata L. (Coleoptera: Coccinellidae)	Competition for food or intra-guild predation
Harmonia axyridis (Pallas) (Coleoptera: Coccinellidae)	Competition for food or intra-guild predation

Case studies provide a starting point for defining qualities associated with biological control agents, and some of these are in the contributions in the remainder of this section (Berkvens *et al.* 2009; Haye *et al.* 2009; Murray *et al.* 2009; Teulon *et al.* 2009). Retrospective analyses where outcomes are known may be able to provide the data for developing ideas about attributes associated with agents perceived to be effective, ineffective and risky. Carefully planned, science-based studies will provide new insights. Furthermore, the study of natural enemy complexes through population interactions (intra-guild interactions) can facilitate determining appropriate attributes (Brodeur & Boivin 2006). In other words, we must learn as much as possible about the biology of candidate biological control agents and the ecological context in which they are used.

CONCLUSIONS.

No comprehensive assessment of characteristics associated with effective, ineffective and risky biological control exists. Clearly, there is a great deal of work ahead. Mathematical models have a use to generate hypotheses and test scenarios but will need to be empirically validated. Case studies are likely to be the source of information for developing databases that can be analysed. It appears that the way forward will be to develop an approach that captures not only the characteristics associated with agents but also the ecological context in which the agents are used.

Only then will we be able to determine principles for guiding decision making on the suitability of biological control agents.

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