If and when successful classical biological control fails

Goldson S.L.1,2*, Wratten S.D.2, Ferguson C.M.3, Gerard P.J.4, Barratt B.I.P.3, Hardwick S.4,
McNeill M.R.1, Phillips C.B.1, Popay A.J.4, Tylianakis J.M.5, Tomasetto F.2

1AgResearch Lincoln, Private Bag 4749, Christchurch 8140, New Zealand
2Bio-Protection Research Centre, PO Box 85084, Lincoln University, Lincoln, 7647, New Zealand
3AgResearch Invermay, Private Bag 50034, Mosgiel 9053, New Zealand
4AgResearch Ruakura, Private Bag 3123, Hamilton 3240, New Zealand
5University of Canterbury, School of Biological Sciences, Private Bag 4800, Christchurch 8140

*Corresponding author

ABSTRACT

Classical biological control of insects has a long history of success, with high benefit-cost ratios. However, most attempts to introduce a biological control agent have been unsuccessful, largely because the agent does not establish in the new environment. This perspectives paper discusses the possibility that even successful biological control may eventually fail, although records show that this is far from a common event. A documented example of eventual biological control failure is discussed and the prospect for future failures analyzed. Part of this analysis is based on an introduced weevil pest in New Zealand and its successful parasitoid biological control agent. The potential fragility of this host-parasitoid relationship is considered as well as why it may indeed be starting to show signs of instability; this is particularly from the point of view of New Zealand’s often species-poor agricultural ecosystems.

1. Introduction

Classical biological control of pest animals, weeds and diseases involves the release of specialist natural enemies of foreign origin in a target species’ ecosystem with the objective
of permanently reducing its numbers and impact. Such a control system can be elegant, self-sustaining, non-polluting and inexpensive – *when it works* (Gurr and Wratten 2000). To this might be added: ‘and as long as it continues to work’. If previously-successful biological control starts to fail, the consequences could be enormous, given the high benefit-cost ratios of many past successes (Page and Lacey 2006; de Clerqet *et al.* 2011). A wide range of factors point to the accelerating need for biological control. Indeed, this requirement continues to grow as world trade and speed of transport systems continue to accelerate and the need to suppress efficiently invasive exotic pest species is greater than ever (e.g. Goldson 2011). However, there are numerous challenges including increasing pesticide resistance in many insect species, more rigorous environmental scrutiny of existing compounds leading to their removal from use, very high registration costs resulting in fewer successful new molecules coming to market and heightened consumer awareness of residues and environmental impacts (Gurr, Wratten and Snyder 2012). Also economic and practical considerations mean that there is demand for self-sustaining solutions to pest problems, such as classical biological control, that do not require frequent and expensive management interventions (e.g. de Schutter, 2010; Wratten *et al.* 2013).

Declining opportunities for conventional solutions is coinciding with human population growth and with this, the demand for what has been referred to as ‘sustainable intensification’ (e.g., Pretty 1997; Godfray *et al.* 2012). Biological control can contribute to this requirement, but since 1880, so-called classical biological control of insect pests has remained at a success rate of around 10% (Greathead and Greathead 2000, in Gurr and Wratten, 2000). If the successful 10% also start to fail, then the consequences could be profound.

Inspite of this low rate, successful classical biological control may to date have appeared to be a ‘magic bullet’ because it can deliver long-term outcomes. However, there is evidence that resistance could arise. For example, Henter and Via (1995a) found significant variation in susceptibility to a parasitic wasp *Aphidius ervi* Haliday *Acrithosiphon pisum* (Harris) clones collected from a single population. The wasps oviposited in aphids from both resistant and susceptible lines, but the eggs failed to develop in resistant hosts indicating that this aphid population has the potential to evolve resistance. However, field-collected material taken in early and late summer, covering several generations, revealed no response to selection by the wasps. The authors speculated that amongst other things, this could have been caused by fitness costs associated with resistance or interference with other control systems. Similarly, Kraaijeveld and Godfray (1997) working on *Asobara tabida* (Nees)
parasitism of *Drosophila melanogaster* Meigen found that the extent to which the latter was selected to invest in defences against pathogens and parasites depended on the advantages that ensue should infection/parasitism occur, but also on the costs of maintaining defences in the absence of these potential selection pressures.

In spite of such examples, there are indeed remarkably few, maybe only one, published examples of successful classical biological control clearly failing through the onset of resistance in the prey/host. Indeed, often where successful classical biological control has not persisted, this has been in conjunction with changed management practices such as altered pesticidal regimes, or changed genetic composition of the control agents through releases of additional strains etc. The former appears to be the case with the biological control of the walnut aphid (*Chromaphis juglandicola* Kaltenbach) by *Trioxys pallidus* Haliday (Aphididae) in California (N. Mills, UC Berkeley; pers. comm.). Also, this process may be occurring in New Zealand with the accelerating use of broad-spectrum pesticides against the recently-colonised tomato-potato psyllid (*Bactericera cockerelli* Sulc.) on solanaceous crops. However, it appears that the only definitive example of the evolution of prey/host resistance occurred in Canada and involved the larch sawfly, *Pristiphora erichsonii* Hartig (Hymenoptera: Tenthredinidae), that was controlled for 27 years by the ichneumonid wasp, *Mesoleius tenthredinus* Morley before failing through widespread host encapsulation of the parasitoid’s eggs (Ives and Muldrew 1984; Dahlsten and Mills 1999). A Bavarian strain of *M. tenthredinis* was later found that could overcome the immune response of *P. erichsonii*, and crosses between the Bavarian and Canadian strains also inherited this ability (Turnock *et al.* 1976). Related to this, Turnock and Muldrew (1971) suggested that the likelihood that resistance of this type will develop can be reduced by providing more than one effective control agent, and recent experimental results support this (Kraaijeveld *et al.* 2012).

Such complexity and infrequency of the occurrence of biological control resistance is in marked contrast to the extent, rapidity and unequivocal nature of the appearance of resistance to pesticides and transgenic pest-resistant crops (e.g. Tabashnik *et al.* 2013). There has been some discussion as to why classical control should be so robust (e.g., Holt and Hochberg 1997). Based on the work of such contributors as Henter and Via (1995a) and Kraaijeveld and Godfray (1997), there are indications of a series of factors that are thought to contribute to biological control stability. A probable important factor is that biocontrol control agents can co-evolve with a pest and thereby counteract resistance developing in the latter (Henter and Via, 1995a, 1995b). Should a pest develop resistance in this way, the former may incur
metabolic or other costs (e.g., a reduction in fecundity) as a consequence (Kraaijeveld and Godfray, 1997). There could also be mechanisms that stabilize susceptibility through the provision of either spatial (e.g., Hanski, 1981) or temporal refugia (e.g., Godfray, Hassell and Holt, 1994). Low disturbance regimes can also preserve biological control effectiveness (e.g., Jonsson et al., 2012). Finally, diverse agro-ecosystems may stabilize biological control, as they often comprise a wide range of natural-enemy guilds that contribute to pest suppression (Tylianakis and Romo, 2010).

Evidence now suggests that at least some of these drivers of biological control stability could well break down. A case study in this context is New Zealand’s pastoral ecosystem. This currently supports high biological control efficacy for several introduced weevil pests (e.g., Barlow and Goldson, 1993; Barker and Addison 2006; Gerard et al. 2011). However, as discussed below, there may now be some reason to look again at the persistence of such success, despite the history of biological control persistence – see earlier. This concern is based on the relatively low alpha diversity of invertebrates in New Zealand’s intensive pastoral ecosystem compared with native grassland systems. The former are effectively incomplete ‘transplants’ of the biodiversity found in the northern hemisphere origin of New Zealand’s pasture plants (ryegrass and white clover) with relatively few New Zealand native herbivorous arthropod species remaining in that environment. Thus, while New Zealand’s farmland may superficially appear similar to large pastoral ‘monocultures’ elsewhere e.g., forb-rich European meadows, the latter include more native and endemic biodiversity, suggesting greater ecological stability and a larger community of biological control agents. In contrast, New Zealand pasture probably has weaker food-web assemblages (sensu Bersier et al. 2002) than in many other regions. These circumstances suggest that in the case of parasitoid-based systems at least, should classical biological control programs begin to weaken through the acquisition of, for example, immune-based pest resistance, then the ‘background biological control’ may not be powerful enough to ameliorate the potential consequences.

Exotic pest populations in New Zealand’s grasslands often build up to very high and damaging densities (e.g., Barker et al., 1989; Goldson et al., 1998; Gerard et al., 2009), probably because of the homogeneity of the pasture ecosystem and absence of species-rich guilds, as discussed above (Goldson et al. 1997). Release from natural enemies in a new range is well known from the invasion literature to facilitate exotic species establishment (e.g. Hong and Stiling 2006). Given that the objective of biological control is to increase the
contribution made to top-down control by enemies such as parasitoids (Stiling and Cornelissen 2005). If classical biological control introductions are carried out carefully, fourth-trophic level hyperparasitoids should not be introduced along with the selected agent. However, the margin for colonization gained through the absence of enemies can come with the negative influence of having to consume novel host/prey resources to which the exotic species is not adapted. Where there are not suitable existing fauna in the receiving area this in turn can impose constraints on success (Parker et al. 2006). Yet in a biological control context, such conditions often no longer apply; rather, exotic consumers have frequently co-evolved with their resource (e.g., introduced parasitoids attacking an invasive pest). In effect, such control agents lack their native suite of enemies, so they receive the benefit of a new host-rich environment, minus the cost. However, when the pest and its biocontrol agents are both accidentally introduced, fourth trophic-level agents often accompany the species in the third trophic level. This is demonstrated by recent work by and Varennes et al., (2014).

2. A New Zealand case study

The general observations on the persistence of biological control, given above, are well exemplified by two exotic weevil species in New Zealand, the Argentine stem weevil Listronotus bonariensis (Kuschel) (ASW) and the clover root weevil Sitona lepidus Gyllenhal (CRW). ASW arrived in New Zealand in about 1910 and CRW around 1995. Due to their ability to reach very high densities (e.g., Gerard et al., 2011; Barker et al., 1989), they are both able to cause very severe damage to New Zealand’s large areas of improved ryegrass/clover pasture (e.g., Prestidge et al., 1991; Barlow and Goldson, 2002). Fortunately, extremely effective biological control occurred via two introduced braconid endoparasitoid species belonging to the genus Microctonus Wesmael. These were M. aethiopoides Loan released against CRW in 2006 (Gerard et al. 2006) and M. hyperodae Loan released against ASW in 1991 (Goldson et al., 1993). Parasitism rates by both these wasp species reached up to 90% shortly after release (Goldson et al., 1998; Barker et al., 2006; Gerard et al., 2011). These rates (e.g., Loan and Lloyd, 1974; Goldson et al., 1990, 2001) and the host weevil population densities (e.g., Goldson et al., 1990, 2001, unpublished data) were much higher than those observed in their centers of origin. In effect, the population dynamics in New Zealand pastures have probably never occurred in the species’ history. This is almost certainly the reason why in New Zealand, observed relict behaviors in exotic pest species appear to confer no adaptive value whatsoever. A good example of this is the continuation of
relict diapause in an environment where there would appear to be no adaptive advantage whatsoever (Goldson and Emberson, 1980).

3. Discussion

As mentioned above, the literature supports the idea that some spatial heterogeneity can lead to the retention of biological control-susceptible genes within the host species (Vermeij, 1985). Similarly, Holt and Hochberg (1997) commented on the importance of spatial structure, where there is a colonizing-extinction cycle across patches of various sizes and distances apart. There are numerous and complex mathematical models describing these sorts of processes that are beyond the scope of this contribution. However, with regard to the discussion to date about the relative dearth of reference to evolved resistance in classical biological control hosts, a major consideration is that in general, such analyses have been based on reasonably diverse, patchy and evolved ecosystems observed elsewhere.

The New Zealand pasture environment therefore provides an interesting contrast to this. It has features that may allow the testing of some of the existing ideas around why resistance to biological control should occur so rarely. Indeed, it can be hypothesized that ASW and CRW resistance to biological control in New Zealand pastoral ecosystems is much more likely to occur than elsewhere, despite the factors listed above that are thought to prevent it. Firstly, co-evolution with the pest is most unlikely if the introduced parasitoids are parthenogenetic, as is the case for both M. hyperodae and M. aethiopoides (Irish strain). Indeed, allozyme data indicate M. hyperodae reproduces by ameiotic thelytoky (i.e., apomixis), so mother and offspring are nearly always genetically identical (Iline and Phillips 2004) with the only possible sources of new M. hyperodae variation being mutation and, perhaps, hybridization. While attempts were made to deliberately introduce some variability within M. hyperodae through the selection of presumed separate geographical populations (Goldson et al., 1993), their adaptive potential is still very likely to be minimal compared to that of ASW. The host undergoes sexual recombination of alleles, even though the population shows little apparent regional genetic variation (e.g. Williams et al., 1994). Secondly, New Zealand’s pastoral ecosystem is anything but heterogeneous either on a small or large scale and this indicates a likely scarcity of refugia in which genetic susceptibility to control agents can be conserved. This means that parasitoids with a high attack rate (sensu Nicholson, 1933) are likely to encounter most if not all hosts, thereby increasing the likelihood of the occurrence of pest
resistance, because of a weak or absent ‘metacommunity’ (Leibold et al., 2004; Urban et al., 2008). Finally, those data that do exist in the literature suggest that resistance to parasitoid biological control agents is most likely when a pest is suppressed by a single agent (e.g., Turnock and Muldrew, 1971; Kraaijeveld et al., 2012); again, this is the situation with the CRW and ASW systems.

The thinking behind this contribution has arisen because there is now the appearance of preliminary evidence that in New Zealand the rates of parasitism of ASW have dropped by as much as 50% over the last 10-15 years. While it is too early for consternation, there is clear reason for further analysis of both the indicative data themselves and the environment in which broad-acre biological classical control operates in New Zealand. The question is, therefore, irrespective of the mechanism, should these first indications of loss of control continue or worsen, then does this fit with one or more of the theoretical considerations developed above? If it does, then it could indicate that the very thing that has led to such outstanding biological control successes, highly invasible species-depauperate and uniform ecosystems, could become the ultimate cause of their failure.

**References**


Loan, C.C., Lloyd, D.C., 1974. Description and field biology of Microctonus hyperodae Loan n. sp. (Hymenoptera: Braconidae, Euphorinae) a parasite of Hyperodes bonariensis in South America (Coleoptera: Curculionidae). Entomophaga 19, 7-12.


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