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General News

The Economics of Rabbit Biocontrol in Australia

A recent economic review[1] estimates that biological control of the European rabbit (*Oryctolagus cuniculus*) in Australia has produced a benefit of at least A$70 billion for the country's cattle and sheep industries over the last 60 years (all figures are in 2011 A$ terms). This includes $54 billion from myxomatosis for the first 35 years after it was released in 1950, and an additional $16 billion from myxomatosis and RHD (rabbit haemorrhagic disease) combined since 1995. The authors used data derived from published literature and developed a loss–expenditure frontier model that incorporates economic data and the cost and efficacy of control to compare marginal changes in losses and expenditure and to explore benefits from releasing biocontrol agents.

The study raises some interesting points about methods for quantifying the benefits of biological control. The authors rejected the use of a 'doing nothing' comparison. Although this may be appropriate in circumstances where biological control is the only likely option, the rabbit situation was and is more complex: not only were control measures already being implemented, but had the myxoma virus failed to establish (as it did in New Zealand), efforts to improve other forms of control would have continued (as they did in New Zealand). A method comparing 'with' and 'without' biological control, was more appropriate, but care needed to be exercised over what 'without' meant because other factors besides biological control influenced the outcome of introducing the myxoma and RHD viruses; government agencies and landholders/farmers took decisions on what more to do (or not do) to augment the impact of the biocontrol agents. In addition, factors other than rabbit control such as improved pasture helped improve productivity. Also, both viruses produce long-term control but, contrary to the conventional classical biological control model, rabbit populations have the capacity to develop disease resistance and saw some recovery after the release of the biocontrol agents.

The authors tried to validate conclusions using published literature and where possible extended the analyses. Using these figures, they estimated (i) savings after the myxoma virus established, (ii) production foregone and increases in control costs as rabbits developed resistance to the myxoma virus and (iii) benefits gained from re-imposed control following RHD establishment. They found that before the myxoma virus was introduced annual losses were in the region of $2 billion. Following the introduction of myxomatosis, rabbit numbers were reduced by 90% and losses were thus reduced to some $200 million for the next decade, although rabbit numbers partially recovered over time. After RHD was established in 1995 (with particular success in dry areas), losses again fell, to $200–207 million, while control costs, which had risen to $600 million by the mid 1990s, fell to $60–70 million. The authors note that following myxoma virus introduction, an 'apparently unavoidable' $200 million annual loss from rabbits was still incurred, and a similar baseline figure emerged after RHD virus establishment; the reasons for the size of this figure are largely behavioural rather than technical, as discussed below.

The authors also reviewed how land manager behaviour changed with biological control. Pre-myxoma virus establishment, most farmers carried out control, usually measures that facilitated harvesting of carcasses and skins, but this was largely abandoned and the rabbit industry shrank by 60% as myxomatosis reduced rabbit numbers. Novel methods of control (e.g. 1080 poison) were not readily adopted because few farmers invested in reducing the 10% remaining rabbits. However, when resistance to the myxoma virus emerged and rabbit numbers increased again, spending on control increased in agricultural areas, although in arid pastoral zones additional control was uneconomic. The authors suggest that this extra effort to control rabbits is reflected in the relatively low and broadly consistent losses despite increasing resistance to the first – and later the second – biocontrol agent that gave rabbit populations the potential to increase.

What also emerged was that when rabbit numbers are relatively low, even in agricultural areas individual land managers accept a trade-off, based on their resources, between control costs and rabbit damage, which partly reflects the existence of populations in hard-to-reach or rarely seen populations and on non-agricultural land such as roadsides. Although the study did not set out to address conservation issues, the authors point out that landholders' reluctance to invest in rabbit control in less accessible or non-agricultural areas puts native biodiversity especially at risk, yet it is unreasonable to expect farmers to bear the whole cost of protecting it from rabbit damage.

The loss–expenditure model indicated that when rabbit numbers fell to relatively low levels after the two biocontrol agents were established, landholders did not always make choices that optimized returns: mopping up the last rabbits is costly, so they do not do it, but this means that the total loss across the country – the 'apparently unavoidable' cost – is substantial. Post-RHD, few farmers in one study, for example, continued with rabbit management even though it appeared to be beneficial; e.g. rabbit warren destruction has high initial costs but provides long-term control, while other measures such as fumigation are effective but labour (= cost) intensive. Subsidies could persuade some farmers, but not all, to undertake further measures. The authors suggest that new criteria are needed for rabbit problems,

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and elimination programmes need to be planned on a landscape scale.

The loss–expenditure frontier model was also used to examine what might have happened if the myxomatosis virus had not established; in doing this the authors assumed that no other method would have been as effective, and that widespread poisoning/trapping/shooting would have been implemented along with harvesting, drawing partly on the New Zealand model with the caveat that the countries are not directly comparable, not least because New Zealand's land has a higher stock-carrying capacity. While they note that this part of the model is 'very much a first approximation', they estimate that expenditure in Australia would have had to have been up to five times as high in the absence of the myxoma virus to achieve equivalent rabbit control. While not wanting to detract from this astonishing contribution of myxomatosis, the authors underline that although the value put on the myxoma virus is very high, this was because it was the first effective control measure against rabbits in Australia. The added value of RHD may seem far less, but had this equally pathogenic agent been established first, the figures could have been reversed. With a cost of $20 million for introducing the RHD virus and its estimated benefit to agriculture of £350 million annually, its cost-effectiveness is clear. From this they argue that estimating overall benefit is more appropriate in economic terms than trying to apportion benefits for each agent.

As rabbit populations slowly increase again as resistance to RHD develops, research into improved control is an urgent necessity. Biological controls take up to 15 years to develop and implement so a long-term view is needed. In the short term, researchers have been looking at other virus variants such as 'RHDVa' which is replacing RHDV in many parts of the world. Such variants might be introduced into Australia relatively easily in a technical sense, being only variants of a virus that is now well established and endemic in wild rabbits. However, experience also shows that it was impossible to introduce new strains of myxoma virus in this way once well-adapted field strains had evolved. Consequently, a second string to the bow involves a wider, worldwide search for other pathogens that might be considered in the long run (see the article that follows).

Importantly, this strategic approach to biosecurity is gaining momentum thanks to initiatives of the Invasive Animals Co-operative Research Centre which brings together industry funds through Australian Wool Innovation and Meat and Livestock Australia, to marshal the technical expertise in state government pest control organizations, CSIRO and Adelaide and Canberra universities in a timely way. Although research funds are always difficult to get, these new innovative approaches to science are proving that important long-term biosecurity issues can still be addressed.

Economic models that demonstrate the long-term economic and ecological benefits of earlier successes in biological control are of course an essential part of assessing where future research investment should be made and are also important in keeping rabbit control high on the Australian political agenda.

[1]Cooke, B., Chudleigh, P., Simpson, S. and Saunders, G. (2013) The economic benefits of the biological control of rabbits in Australia, 1950–2011. *Australian Economic History Review* 53(1), 91–107.

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Desktop Surveys: Using Social Media in Rabbit Biological Control

Social media and other informal online information resources are beginning to be exploited as a novel method of surveying for biocontrol agents by scientists involved in the Australian rabbit biological control programme outlined at the end of the preceding article.

David Peacock (Biosecurity South Australia) is one of the scientists involved. Part of his search methodology involves passive monitoring and horizon scanning of wildlife health and disease networks and RSS feeds (which is being undertaken by the Australian Wildlife Health Network) in the hope of detecting any international outbreaks of disease in the European rabbit.

Australia's current strategy for classical biological control of rabbits was outlined in a 2008 paper[1], which stated that 'The most cost-effective method for finding potentially useful but as-yet undiscovered [biocontrol agents] would be to maintain a global watch on new diseases and pathologies in domestic rabbits.' The argument for global monitoring is illustrated by the provenance of the two existing biocontrol agents in Australia: the myxoma virus, the first biocontrol agent for rabbits introduced to Australia, arose in Uruguay where it was first identified in 1896, while the second, rabbit haemorrhagic disease virus, was identified for the first time in China in 1984.

The authors identified a range of potential sources of new biocontrol agents, including: (i) worldwide, domestic rabbits kept in laboratories or commercial warrens or as pets – intensively managed rabbits are useful as 'sentinels' because new diseases are more easily spotted than in wild populations, (ii) rabbits in their natural range in Europe, (iii) European rabbits in their introduced range, (iv) areas where other lagomorphs were introduced and European rabbits persist, such as *Sylvilagus* to European hunting reserves where rabbits were depleted by myxomatosis, (v) areas where introductions of the European rabbit failed despite climatic suitability, such as North America and southern Africa (was some as-yet unknown pathogen responsible?), and (vi) other lagomorphs anywhere, but especially those closely related to the European rabbit and in climatically similar areas.

Potential agents could include rabbit pathogens from the area of origin that were not introduced with rabbits into Australia, new strains of known diseases, pathogens newly acquired by rabbits in their introduced range (host-specific ones are most likely to be found where there are native lagomorphs), and pathogens found in related lagomorphs that might cause disease in rabbits.

Australian scientists are already working on potential agents from some of these sources, but are keen to learn of new ones. The pathogens do not necessarily need to cause high mortality to produce useful reductions in population fitness.[1] If anyone anywhere in the world can suggest pathogens that the Australian team should examine or consider, please contact David Peacock (contact details below).

[1]Henzell, R.P., Cooke, B.D. and Mutze, G.J. (2008) The future biological control of pest populations of European rabbits, *Oryctolagus cuniculus*. *Wildlife Research* 35, 633–650.

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Bougainvillea Mealybug in Spain: a Case of Fortuitous Biological Control

That bugbear of plant protection, the unregulated horticultural trade, has been responsible for introducing many invasive pests of ornamental plants around the world. For a number of reasons, including fortuitous biological control, the number of species actually introduced probably far exceeds those that have gone on to become notorious. According to a recent study in Spain[1], the bougainvillea mealybug, *Phenacoccus peruvianus*, which was introduced from South America to Almería in eastern Spain via this pathway in 1999, may become one of the former. Since its introduction it has spread rapidly in the western Mediterranean and is now naturalized widely along the Mediterranean coast of France, Monaco, Spain, the southern coast of Portugal, the Balearic Islands, Corsica and Sicily. It has otherwise been recorded in the wild only from Peru and Argentina, in its area of origin; a single species was described on the basis of specimens from these countries by Granara de Willink in 2007.

The species is commonly known as the bougainvillea mealybug because of its preference for this host, but occurs on woody plants, including other well-known ornamental genera, belonging to nine families and has also recently been reported from two crops: Acanthaceae (*Justicia*), Amaranthaceae (*Alternanthera*), Asclepiadaceae (*Araujia*), Asteraceae (*Baccharis*, *Eupatorium*), Aucubaceae (*Aucuba*), Myoporaceae (*Myoporum*), Nyctaginaceae (*Bougainvillea*), Scrophulariaceae (*Budleja*) and Solanaceae (*Cestrum*, *Solanum* including tomato, also *Nicotiana* – tobacco).

There is little information on the economic status of *P. peruvianus*, which causes significant aesthetic damage to ornamental bougainvillea in particular and reduces its market value. Large mealybug populations cause foliage necrosis, leaf loss and dieback, and fungi grow on the honeydew. *Phenacoccus peruvianus* is not accorded pest status by the European Commission; it is not recommended for quarantine pest regulation by EPPO (European and Mediterranean Plant Pest Organization) nor is it on its alert list. Bougainvillea plants are thus moved freely between European Union countries, so its further spread is inevitable. Light or early infestations are difficult to detect so eradication is likely to fail, and the mealybug's cryptic nature makes chemical control difficult. In Europe, mealybugs are one of the commonest invading groups (along with two other plant-feeding Hemipteran groups, aphids and diaspids); the 37 alien mealybug species represent a quarter of the described mealybug fauna of Europe. Invasive mealybugs have, however, been the subject of some exceptionally successful classical biological control programmes.

The emergence of a new plant pest can provoke a flurry of taxonomic activity; kept in check in its home range by natural enemies, it may have been overlooked and/or the biodiversity of the area of origin may not be well described. *Phenacoccus peruvianus* was described only in 2007, some years after its introduction to Europe. The delay in identifying a new pest causes inevitable delays to starting a biological control programme, and biological control had not been considered for *P. peruvianus*, largely because nothing was known about its natural enemy complexes in Europe and South America. However, the activities of parasitoids and predators in the introduced range are not hampered by formal identification; new associations may be formed, or serendipitously introduced natural enemies may attack the potential invader. According to the authors there are at least six previously reported cases of fortuitous biological control of mealybugs by accidentally introduced natural enemies.

In the Spanish study, which is published in *BioControl,* the impact of the local fauna on *P. peruvianus* was investigated by surveying *Bougainvillea glabra* and/or hybrid *B. glabra* × *buttiana* in six urban 'green spaces' in València, where the pest was first reported in 2005 and population levels were high when the study began. Surveys were conducted weekly-to-monthly over three seasons, from March 2008 to September 2010. Samples were scored for mealybug density; they were also inspected for signs of developing mummies, and these were kept and any emerging parasitoids identified. Predators found during surveys were captured and identified.

In all years, *P. peruvianus* populations increased in spring, reaching a peak in June/July, but peak numbers in 2009 and 2010 were only 40% and 20%, respectively, of the population peak in 2008, while numbers of parasitoids were significantly higher in each successive year. Of the three encyrtid parasitoids and three pteromalid hyperparasitoids recovered, the most abundant species overall (91.6% of specimens over the three years) was the gregarious parasitoid *Acerophagus* n. sp. near *coccois*, which was recovered from all sites, parasitizing second and third instar nymphs and adults. However, the relative abundance of parasitoid species varied over the study: in 2008 a second but solitary encyrtid, *Leptomastix epona*, comprised 28.2% of emerged parasitoids and *Acerophagus* sp. 47.7%; by 2010 *Acerophagus* comprised 97.9% of specimens and *L. epona* only 0.5%. *Leptomastix epona* is a native generalist parasitoid that has also been recovered from another new Nearctic invasive mealybug in southern Spain, *Phenacoccus solani*. The most abundant hyperparasitoid, *Pachyneuron* sp. (probably a hyperparasitoid of *L. epona*), decreased from 23% of total specimens in 2008 to 1.0% in 2010. Some generalist predators were also found on *Phenacoccus peruvianus* eggs and nymphs, particularly coccinellid beetles, but the major natural enemy was the as-yet undescribed *Acerophagus* sp.

The authors conclude that the decrease seen in *P. peruvianus* populations in València from 2008 to 2010 can be attributed to *Acerophagus* sp. The argument receives support from the observation that in the first year of the survey, high *P. peruvianus* populations were maintained through the season until *Acerophagus* sp. became the major parasitoid in September, while in the subsequent years *Acerophagus* sp. was abundant, and the dominant parasitoid, from spring onwards and *P. peruvianus* populations were smaller. The authors suggest that *Acerophagus* sp. may have been accidentally imported when *P. peruvianus* was introduced, or shortly after. As the parasitoid is previously unknown from the Mediterranean region, this study raises the possibility that *P. peruvianus* may be controlled more widely under Mediterranean conditions by the encyrtid.

Two other interesting observations emerged from the study. Firstly, only female *Acerophagus* sp. were recovered, which would be the first report of parthenogenesis in this genus. Secondly, host density and rate of parasitism were negatively correlated on bougainvillea, with parasitism by *Acerophagus* sp. decreasing as the mealybug abundance increased; possible explanations include ant disturbance related to the lengthy oviposition behaviour of this encyrtid, and catastrophic patch failure where high infestations lead to leaf fall.

[1]Beltrà, A., Tena, A. and Soto, A. (2013) Fortuitous biological control of the invasive mealybug *Phenacoccus peruvianus* in southern Europe. *BioControl* Online First. DOI: 10.1007/s10526-012-9488-5.

Additional sources: www.fera.defra.gov.uk

Beltrà, A., Soto, A., Germain, J.-F., *et al.* (2010) The bougainvillea mealybug *Phenacoccus peruvianus*, a rapid invader from South America to Europe. *Entomologia Hellenica* 19, 137–143.

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Smothering Parthenium Weed Boosts Biological Control

Research in Queensland, Australia, indicates that integrating selected suppressive plant species with biological control enhances control of the invasive neotropical weed *Parthenium hysterophorus*[1].

Parthenium is a weed of rangelands and crops, disrupts biodiversity in natural ecosystems, and is a health hazard to people and domestic and wild animals. It is a weed in parts of Asia, Africa and Australia. In Queensland, where most work on biological control has been done, it infests 600,000 km^2 of pastureland. The stem galling moth *Epiblema strenuana* and the leaf feeding beetle *Zygogramma bicolorata* are the two most prominent of the established bicontrol agents, reported to reduce parthenium plant height by 40%, flower production by 82% and soil seed banks by 70%, while the stem boring weevil *Listronotus setosipennis* and the rust pathogen *Puccinia abrupta* are also present although their impact is not quantified.

It has long been recognized that biological control will not provide a complete solution to parthenium weed. Efforts to develop an integrated approach in Australia have assessed how quarantine measures, seed spread prevention, grazing land management, fire and chemical control could complement biological control. Physical and manual control have been widely used in Asia and Africa.

Attempting to suppress parthenium weed using competing plants has not been tried to any extent, although introduced and native pasture species have been identified in Australia that can reduce parthenium shoot mass by at least 50% and produce palatable fodder. The concept of combining biological control with a pasture species is an attractive one: the ideal outcome would be enhanced impact on the weed over that achieved by either acting alone, while also producing a fodder crop. Previous work in other systems suggested that the outcome of the interaction will vary depending on the suppressive plants and herbivorous insects used.

Shabbir and co-workers looked at how biocontrol agents and pasture species alone and in combination affected parthenium weed, and how biocontrol agents affected fodder production. They assessed the impact, under field conditions over two years, of the biocontrol agents at natural densities and of six pasture plants sown in individual species plots. The most prevalent biocontrol agent in year one was *E. strenuana*, followed by *Z. bicolorata*, *L. setosipennis* and *P. abrupta*. In year two, *Z. bicolorata* was present throughout the summer but *E. strenuana* only very late in the season, and the other two agents were absent. The pasture species, selected on the basis of suppressive ability in greenhouse trials and high yielding capacity, were the native species bull Mitchell grass (*Astrebla squarrosa*) and kangaroo grass (*Themeda triandra*), and the introduced species purple pigeon grass (*Setaria incrassata*), buffel grass (*Cenchrus ciliaris*), seca stylo (*Stylosanthes scabra*) and butterfly pea (*Clitoria ternatea*).

Results indicated that the pasture species and biocontrol agents acted synergistically to reduce parthenium above-ground biomass. Despite the variation in biocontrol agent presence, these alone reduced weed biomass by 35% and 37% in years one and two, and the various suppressive grasses reduced it by 18–51% and 23–67%. Together they reduced it by 60–86% and 47–91% in the two years. The impact of biocontrol agents on suppressive plant biomass was similar in the two years of the trial: biomass was 6–21% and 6–23% greater than in the absence of the parthenium natural enemies; one of the three most productive species was the native kangaroo grass.

The authors conclude that biological control agents and suppressive plants can be combined successfully to improve the management of parthenium weed to a level that is better than either management option alone. They highlight the promising finding that the native species – and particularly kangaroo grass – were able to suppress parthenium weed, counter to the common finding that natives do not compete effectively with invasive plants. This suggests that careful assessment of potential fodder species will pay dividends.

[1]Shabbir, A., Dhileepan, K., O'Donnell, C. and Adkins, S.W. (2013) Complementing biological control with plant suppression: implications for improved management of parthenium weed (*Parthenium hysterophorus* L.) *Biological Control* 64(3), 270–275.

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Using Land Management and Crop Rotations to Enhance Biological Control

A study in *Journal of Applied Ecology*[1] has separated the effects of landscape complexity and crop rotation on biological control by parasitoids and predators in one agricultural system, and as a result shows how management at these two levels might be used to stabilize and enhance natural pest control.

The field experiment took place in spring barley fields in southern Sweden. Proportion of ley (i.e. rotational crops cultivated for grazing or fodder) was used as a proxy for crop rotation and crop diversity at the landscape level; landscapes with larger proportions of ley support longer and more diverse rotations. The proportion of pasture (i.e. fairly permanent semi-natural unfertilized grassland) and the length of field borders were combined and used as a proxy for landscape complexity; pasture is used only for grazing and is less intensively managed than crops. Pots of spring barley that had been infested in the laboratory with late-instar apterous aphids (*Rhopalosiphum padi*) were placed at the soil level at the edges of selected fields for five days during summer, with presence or absence of cages being used to exclude or allow natural enemy access.

In line with findings from other studies of this system, natural enemies had a strong impact on aphid numbers. Overall biological control was best predicted by landscape complexity while crop rotation had no measurable effect. Mean parasitism (as distinct from predation) was low, possibly related to the timing of the experiment, and there were no discernible landscape or crop-rotation effects. However, crop rotation affected variability in both overall control and rates of parasitism; it was higher for both in longer and more diverse rotations, indicating that they provide less stable control than short, less diverse rotations.

Thus in the spring barley system in Sweden, biological control is most effective in complex landscapes with repetitive, short crop rotations, and least effective in simple landscapes with more diverse crop rotations that include perennial crops. The authors express surprise that they did not find evidence for an impact of crop rotation intensity on overall pest control, but conclude that landscape complexity is the main determinant for biological control in this system. They suggest that similar studies of other pests in other crops would help to build a broader picture of how landscape effects and crop rotation interact and affect biological control by natural enemies.

The study also allowed the impact of the two measures to be assessed across different spatial scales (0.5–3.0 km). The results indicated that biological control was best predicted by landscape complexity at a relatively small (0.5–1.0 km) scale, while stability was least in longer and more diverse rotations at the 2.5–3.0 km scale. The authors use these findings to argue for the conservation of heterogeneous landscapes, characterized by a high proportion of semi-natural habitats such as pastures and relatively small fields, in order to maintain and enhance effective biological control in agroecosystems.

[1]Rusch, A., Bommarco, R., Jonsson, M., Smith, H.G. and Ekbom B. (2013) Flow and stability of natural pest control services depend on complexity and crop rotation at the landscape scale. *Journal of Applied Ecology* 50(2), 345–354.

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Biocontrol Agents: Strength in Numbers or Two's a Crowd?

It is an axiom of biological control that although 'silver bullet' agents are welcome, they are very rare. The average classical biological control programme today typically sets out with the expectation that a number of agents, ideally a small suite of complementary species, will need to be introduced to bring about a useful reduction in the target population. However, predicting what and how agents will complement each other is problematic. Few studies have attempted a general analysis although research, usually retrospective, has been published for specific systems.

A review published in *Proceedings of the Royal Society B*[1] presents a 'vote-counting' and meta-analysis of 74 unique host-plant-plus-two-natural-enemies combinations (45 with two arthropod natural enemies, 22 with an arthropod and a pathogen, and seven with two pathogens), taken from 51 studies, to investigate: (i) the prevalence of non-independent effects of two natural enemies on a shared host, (ii) whether on average natural enemies reduce plant performance (using meta-analysis), and (iii) whether specific experimental factors or plant or natural enemy attributes are associated with non-independence. Some of the natural enemies considered were actual or potential biocontrol agents of weeds, but others were pests/pathogens of crops or occur in natural ecosystems. Aspects of plant performance measured included alterations in various vegetative parts, reproductive output and mortality for individual plants and only occasionally plant density, although such population-level effects are more useful as measures of biological control. Of the natural enemy pairs in the meta-analysis, 32 were both specialists, 18 had one specialist and one generalist, and 15 were both generalists.

Using multiplicative and additive models, the authors found that natural enemies had independent effects on plant performance in 77% of response measurements. Between 14% and 22% were antagonistic ('multiple enemies had less effect on plant performance than predicted') and the remainder were synergistic. Effects of combined natural enemies on host plants were less than for one agent acting alone in 5–7% of cases overall (or c. one-third of the antagonistic interactions) although it is not clear how many of these were biocontrol agents; they had more effect in 8–15% of all responses. No significant differences were found for specialist cf. generalist combinations or arthropods cf. pathogens. The meta-analysis found that although multiple (two) natural enemies in the studies had independent effects on plant performance in most cases, antagonistic effects occurred particularly when the natural enemies (i) attacked the same part of the plant concurrently or (ii) attacked reproductive structures. For these reasons, antagonistic interactions were found disproportionately in Asteraceae and with dipteran natural enemies. No robust predictors of synergism were found.

The analysis did not focus specifically on biocontrol agents, but the authors discuss its implications for the discipline, and suggest, 'two simple rules: (i) avoid introducing species that attack the same part of the plant at the same time, and (ii) assess the impact on plant performance of species attacking reproductive structures in conjunction with existing agents.'

Although meta-analyses can be useful because they show overall patterns that can be helpful in guiding decisions (e.g. for biocontrol agent prioritization), at the same time they should be treated with care at the individual project level because other criteria (such as host specificity) might be more important, or the patterns found might simply not apply to a particular project.

The finding that natural enemies attacking the same plant parts interfere with each other is not surprising: a leaf pathogen may leave less foliage for an insect defoliator to attack, and vice versa. It is generally assumed that an ideal suite of biocontrol agents attack different parts of the plant, so the first rule coincides with ideal practice. However, the paper could be seen to be missing the point of biological control as a practical discipline where the aim is to control the target weed, rather than as an exercise in meeting predictions. On the other hand, the authors may be working on the principle that programme resources are limited and each biocontrol agent's impact should be maximized. Reality probably falls between the two. The identified weaknesses in the predictions for the two categories above indicate that research is needed to improve predictability of outcomes so that decisions are better informed. Of particular interest is the finding that, in a minority of cases, pairs of natural enemies did less damage than a single one and lessons could be drawn from these studies. However, for the majority of cases where antagonism occurred, two species had more impact than one. It does not necessarily follow that agent combinations would not be sanctioned for release on the grounds that the combined impact is likely to be lower than previously thought. A modest add-on impact of a second agent may still be significant in terms of controlling the weed.

There are other practicalities to be considered: when a programme begins, little or nothing may be known about potential biocontrol agents for the target weed. Particularly when the weed has a large native range, surveys may extend for years, often well beyond the introduction of the first agent. Alternatively, where introduced agents have failed to make expected and sufficient impact, further surveys may be instigated. Should an agent found during later surveys, which meets host-specificity criteria and inflicts significant damage on the target weed in the home range and laboratory trials, be rejected on the grounds that it may reduce stand-alone damage inflicted by what appears from the evidence to be a less-effective but previously introduced agent attacking the same plant part? Moreover, reasons for promising agents having disappointing impact are often poorly understood, if at all, so there should be caution in overemphasizing the role of antagonism between agents.

The second rule, on releasing agents attacking reproductive structures, is understandably cautiously worded. In many cases – where target weeds only reproduce by seeds or where plants are probably seed-limited – biocontrol agents that reduce reproductive output have a clear role. In addition, in cases of conflict of interest, where reduction of spread is often the compromise (as for weedy acacias in South Africa historically and Russian olive in North America currently), they are seen as agents of choice. The paper did not have the remit to consider conflicts of interest, but publications can be hijacked by parties with different agendas. Again, it is not surprising that natural enemies attacking different reproductive structures affect each other; if a fungus or insect has destroyed a lot of the flowerheads, there will be fewer seeds for agents that attack that stage. In practice other issues may be more pertinent, for example, many seed-feeding insects are highly host specific and this is likely to be of more over-riding interest to agencies considering biocontrol agent introductions than whether the sum of two seed feeders' impacts is predicted to be either modestly or much greater than that of the agents acting alone.

A balance needs to be struck. In an ideal world the agent predicted to be most effective would be released first, but in practice biocontrol scientists work with the agents they have at the time. The authors' aim is to contribute to identifying what to do *in* the ideal programme so that each programme can maximize the number of ideal things that it does.

[1]Stephens, E.A.E., Srivastava, D.S. and Myers, J.H. (2013) Strength in numbers? Effects of multiple natural enemy species on plant performance. *Proceedings of the Royal Society B* 280, 20122756. http://dx.doi.org/10.1098/rspb.2012.2756

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Prepared with assistance from CABI's weed biological control staff.

Chemical Ecology and Weed Biological Control

A review of the literature relating to plant secondary metabolites from the perspective of weed biological control indicates that the interface between the two disciplines 'presents a rich opportunity to exploit potentially coevolved relationships between agents and plants where chemical factors mediating interactions are important.'[1] Unravelling the chemistry is only part of what is needed, and the authors stress that more interaction between biocontrol scientists and those working in chemical and other areas of ecology would have two-way benefits.

Chemical ecology has an important role in invasive species science as 'the study of the chemical interactions between organisms and their environment [which also] seeks to examine the production of and response to signaling molecules or semiochemicals and to decipher the information content of the mediating compound.' Its significance for classical weed biological control is in explaining the role of plant secondary metabolites in host specificity. The primary role of plant secondary metabolites is to deter animal species from feeding on the plant producing them, but during the coevolutionary arms race, host-specific species have evolved to not only tolerate such chemicals, but also exploit them as one of a large number of host-finding cues – thus turning the plant's use of secondary metabolites on its head – while some plant-feeding species sequester them as part of their own defence system.

The review considers the status of the application of chemical ecology in weed biological control and identifies areas where the fields can be integrated to provide better predictions of host range, establishment, and impact on target weeds. Five overlapping topics are covered (i) the chemistry of host specificity in biocontrol agents, (ii) evolutionary changes in secondary plant chemistry and effects on biological control, (iii) herbivore induction of secondary plant compounds in relation to biological control, (iv) intraspecific variation in secondary plant metabolites, and (v) herbivore sequestration of plant secondary metabolites as a defence against natural enemies.

The centrifugal basis of host-specificity testing stands the chemical ecology test at higher levels, but some anomalous findings at the genus/species level suggest that testing responses to a few well-known groups of chemicals may not always be adequate; a more holistic metabolomics approach would be the ideal, although it would be challenging to implement. Care should also be taken to study the different steps in the host-location process. In terms of what other disciplines can gain, the authors point out that biological control programmes are a good opportunity to assess ecological theory relating to the evolution of increased competitive ability/shifting defence hypotheses, and indeed the above theories have sprung from biological control systems. Currently the evidence in the literature supporting them is mixed, although some of the most successful weed control projects provide strong evidence in support. Induced chemical defences in crops are potentially a novel tool for pest control but are likely to have an impact on biological control and information is as yet patchy. They have been studied in a number of biological control systems, where impacts on biocontrol agents seem to vary, and more research is needed. Intra-species variation is also a topic with a poor knowledge base although chemotypes of some weed species have been characterized along with their effects on biocontrol agents, and a range of volatiles has been described from others. The fifth topic covered, sequestration, also suffers from a paucity of information. It could be a useful tool for biocontrol scientists who are nowadays under pressure to identify agents most likely to be effective; a species that sequesters host plant chemicals is likely to be less palatable to generalist predators, but how much weight this would or should be given in the prioritization process is difficult to assess.

Besides identifying where the knowledge gaps lie, the enduring message from this review is that we should consider chemical ecology more than we have in the past, particularly when interpreting results from pre-release host-range testing and when predicting the dynamics of biocontrol agent–weed interactions in the introduced range.

[1]Wheeler, G.S. and Schaffner, U. (2013) Improved understanding of weed biological control safety and impact with chemical ecology: a review. *Invasive Plant Science and Management* 6(1), 16–29.

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Where Aphids Fear to Tread

An open-access article in *Biological Control*[1] provides the first evidence that tracks left by an arthropod predator can be used by herbivores to assess predation risk and avoid plants visited by predators. Most animals have evolved behaviour that decreases the risk of being found by a predator.

Most of the work on aphids has focused on behaviour related to attack or close contact with the predator. This study investigated whether the bird cherry–oat aphid (*Rhopalosiphum padi*) could detect semiochemicals from an important predator, the seven spot ladybird (*Coccinella septempunctata*). A fair amount of research has been done on ladybird semiochemicals, but in relation to intraspecific and intraguild competition.

In this study, apterous *R. padi* reared on barley in greenhouse conditions were tested against field-collected *C. septempunctata*. Experiments included a no-choice test to assess aphid settling on plants previously visited by ladybirds, and a set of choice tests to investigate whether previous presence of ladybird larvae or adults affected aphid preference, how long this effect lasted after they were removed, and whether tracks alone cf. tracks plus faeces were sufficient to elicit a response. An olfactometer was used to test aphids' reaction to adult and larval ladybird volatiles, including presence, previous presence and tracks-only conditions.

No-choice results indicated that aphid settling was reduced (40–53%) on plants where ladybirds had been present. Choice results showed that aphid avoidance increased with higher numbers of ladybirds, and females in particular – an effect that was also found in the tracks-only test. The response decreased over time, and took longest (six days) to decay for females. Olfactometer results indicated that aphids showed greater avoidance behaviour to volatiles with a larger number of adult ladybirds or their residues, and again the effect was most marked with female ladybirds, a result again replicated in the tracks-only condition. However arrestment/attractant responses were observed with a low number of all stages and both sexes.

The authors conclude that aphids may be able to use the semiochemical contact or olfactory cues, or both, left by ladybirds walking on a potential host plant to assess the risk of predation – from ladybird numbers, sex and time since they were there – to decide whether to settle and deposit nymphs, or not. The authors suggest that this mechanism may have an important role to play in the biological control exerted by ladybirds on aphid populations.

[1]Ninkovic, V., Feng, Y., Olsson, U. and Pettersson J. (2013) Ladybird footprints induce aphid avoidance behaviour. *Biological Control* 65(1), 63–71.

Parasitoids Drive Fruit Flies to Drink

Scientists at Emory University in Atlanta, Georgia in the USA have described a novel behavioural immune response by which *Drosophila melanogaster* fruit flies protect their offspring from endoparasitoids[1]. They describe how flies that encounter endoparasitoids switch to laying eggs in alcohol-laden food to increase survival rates in the offspring. Maximum survival rates for *D. melanogaster* larvae in the absence of parasitoids are around 90%. They are as low as 10% in the presence of parasitoids, but may rise to over 50% where eggs are laid in alcoholic substrates.

The authors had previously shown[2] that (i) fly larvae living in alcoholic environments are parasitized less often, and (ii) for parasitized individuals, the increased haemolymph alcohol levels found in fly larvae feeding on alcoholic media kills developing endoparasitoid larvae, with higher levels of alcohol having a greater effect. Consequently, despite some ethanol-mediated fly mortality, more flies and fewer wasps eclosed than in a zero-alcohol treatment. The study also showed that these effects are more pronounced for the figitid generalist *Leptopilina heterotoma* than for the *D. melanogaster* specialist *L. boulardi*.

In their new study on fruit fly adults[1], the authors presented flies with two food sources, containing either 6% or 0% alcohol, and observed their behaviour in the presence or absence of different parasitoid species/sexes. In the absence of *L. heterotoma*, 60% of fruit flies preferred the non-alcohol substrate for oviposition and fly larvae developing in that substrate did so at a faster rate than those in alcoholic substrate. But when female parasitoids of this species were present, 90% of flies laid their eggs on the alcohol-laced substrate; in this situation, fly larvae developing in the alcoholic substrate fared the better in terms of survival.

The behavioural response turned out to be very specific. Female *D. melanogaster* did not change their oviposition behaviour if male *L. heterotoma* or pupal parasitoids were present (egg-laying behaviour probably has little impact on pupation site), but they did in the presence of four other larval endoparasitoids (two other *Leptopilina* spp. and two braconid species). Flies exhibited the behavioural change even though they had been bred in a laboratory parasitoid-free environment for generations. The authors conclude that there is an innate behavioural mechanism broad enough to recognize two families of larval endoparasitoids, but specific enough to distinguish pupal parasitoids, and male from female endoparasitoids.

Experiments into the underlying mechanism found that vision was critical: mutant blind flies did not respond to female *L. heterotoma*, while mutants unable to detect odours did. The effects on oviposition persisted in fruit flies exposed to female *L. heterotoma* for several days after the parasitoids were removed. Investigations into the neurological basis of the behaviour showed that two proteins implicated in alcohol seeking and in long-term memory were also implicated in alcohol preference/tolerance during the behavioural immune response.

When the authors tested six other *Drosophila* species, they found that three species that tolerated high alcohol levels exhibited similar behaviour, while three species that were intolerant of alcohol did not, suggesting that adapting to an alcoholic environment has allowed the behaviour to evolve multiple times in the genus.

[1]Kacsoh, B.Z., Lynch, Z.R., Mortimer, N.T and Schlenke, T.A. (2013) Fruit flies medicate offspring after seeing parasites. *Science* 339(6122), 947–950.

[2]Milan, N.F., Kacsoh, B.Z. and Schlenke T.A. (2012) Alcohol consumption as self-medication against blood-borne parasites in the fruit fly. *Current Biology* 22, 488–493.

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South Africa's Century of Weed Biocontrol

An article by Hildegard Klein in *Plant Protection News*[1] celebrates the centenary in 2013 of the first introduction of a classical biological control agent for a weed in South Africa. *Opuntia monacantha* was invading coastal areas of KwaZulu-Natal and the Eastern Cape. The biocontrol agent was the host-specific cochineal species *Dactylopius ceylonicus*, obtained from India via Sri Lanka, courtesy of the Queensland Prickly Pear Commission. The success of control was complete and has continued to this day.

Since then South Africa has become one of the world's leading countries for weed biological control, in terms of both science and practice. In the past 100 years, some 75 biocontrol agent species or biotypes have become established in South Africa on 50 invasive alien plant species, with complete or substantial levels of control in 30 of them and estimated benefit:cost ratios in the range 8:1 to 3726:1.

[1]Source and further information: Klein, H. (2012) A century of biological control of invasive alien plants in South Africa. *Plant Protection News* No. 94, pp. 1–2. Newsletter of the Plant Protection Research Institute (PPRI), an institute in the Natural Resources and Engineering Division of the Agricultural Research Council (ARC).
Web: www.arc.agric.za/home.asp?pid=1&toolid=2&sec=774

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Biological Control Programmes in Canada Series

The Entomological Society of Canada has obtained copyright permission to publish the first three volumes of the 'Biological Control Programmes in Canada' series on its website as downloadable PDF files. The first volume deals with years up to 1958, with subsequent volumes covering the years 1959–68 and 1969–80.

The fourth volume (1981–2000) is available from CABI in print and ebook versions, while the fifth volume (2001–12 is due out this year from CABI.

Web: www.esc-sec.ca/cabi.php
http://bookshop.cabi.org/

ISBCW Proceedings

The proceedings of the XIII International Symposium on Biological Control of Weeds, held in September 2001 in Hawaii, have been published[1]. They include 36 papers, 183 abstracts, and five workshop summaries. Nine chapters cover symposium themes/sessions and a last one deals with the workshops. The proceedings will be posted online at: www.invasive.org/library/index.cfm

Copies will be sent to all participants; queries: Tracy Johnson (tracyjohnson@fs.fed.us) or Sharlene Sing (ssing@fs.fed.us). A limited number of extra hard copies is available; contact: Richard Reardon (rreardon@fs.fed.us) or Yun Wu (ywu@fs.fed.us).

[1]Wu, Y, Johnson, T., Sing, S., Raghu, S., Wheeler, G., Pratt, P., Warner, K., Center, T., Goolsby, J. and Reardon, R. (eds) (2013) *Proceedings of the XIII International Symposium on Biological Control of Weeds.* USDA Forest Service, FHTET-2012-07. 530 pp.

A Future for Bionematicides

The US Environmental Protection Agency (EPA) has recently granted registration approval to Syngenta for a bionematicide seed treatment against the soybean cyst nematode (SCN). SCN is responsible for growers' losses amounting to US$1.5 billion annually as the pest has become a widespread problem across all major production areas in the US Midwest. The new product is based on the bacterium *Pasteuria* and is expected to be commercialized for the 2014 growing season.

While this is welcome news, biological control products for nematodes could be even more numerous, according to a paper in *BioControl*[1]. The authors review recent developments in the commercialization of bionematicides, highlighting that four key ingredients are being backed by large international companies and are likely to result in new products in the near future. However, while *Pasteuria* spp. And *Purpureocillium lilacinus* have been intensively studied as potential nematicides, little research has been conducted on *Bacillus firmus* and *Myrothecium verrucaria* fermentation products, which also have promise as commercial bionematicides. By surveying the trade press the authors found evidence that these second two agents, particularly *B. firmus,* are the most widely used. As research priorities, they say there is a need to further understand the ecology and mode of action of *B. firmus* when used as a bionematicide. In addition, while all four active ingredients have been shown to be effective in laboratory and/or small plot trials, there are few independent data supporting product efficacy in target markets.

[1]Wilson, M.J. and Jackson, T.A. (2013) Progress in the commercialisation of bionematicides. *BioControl* Online First. Forum Paper, March 2013.