

Biocontrol Files

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Canada's Bulletin on Ecological Pest Management



Special issue on invasive species

Managing Invasive Species with Biological Control

Invasive alien species are one of the leading threats to biodiversity. They also impose enormous costs on human health and on agriculture, forestry, fisheries and other human enterprises. These species are mostly introduced as a result of human activities. Rapidly accelerating trade, tourism, transport and travel over the past century has dramatically enhanced the spread of invasive species, allowing them to surmount natural geographic barriers.

Invasive alien species are often controlled in their original range by a combination of competition for resources and their natural enemies. They are usually introduced into new environments without these natural enemies. Freed of their parasitoids, parasites and predators, and in communities that have little ability to compete with them, alien species often grow and/or reproduce more vigorously in the country of introduction. Natural enemies for introduction are selected on the basis of their host specificity to minimize or eliminate any risks of effects on non-target species.

In comparison with other methods, classical biological control is, when successful, cost-effective, permanent and self-sustaining. It is ecologically safe due to the high specificity of the agents used. The main disadvantages are the lack of certainty about the level of control that will be achieved and the delays until the established agents achieve their full impact.

There has been a lot of debate in recent years about the safety of classical biological control, particularly with regard to the potential of introduced biological control agents to have adverse effects on non-target organisms. In particular, some of the introductions made over 50 years ago were of generalist predators, including vertebrates such as mongoose and cane toads which have had severe adverse effects on non-target populations, including species of conservation importance.

However, today the safety standards of biological control are very rigorous. It is a normal requirement to assess the specificity of all agents proposed for introduction. This involves extensive laboratory and field screening tests. An informed decision can then be made by the appropriate national authority, taking into consideration the potential for any effects to non-target organisms.

While biological control is highly recommended to control an established population of an invasive alien species, eradication cannot be expected. Rather, the aim is to reduce an invasive species' population to levels where the populations of prey/host and predator/parasitoid are in a dynamic balance. ■

Adapted from Invasive Alien Species: A Toolkit of Best Prevention and Management Practices, Edited by Rüdiger Wittenberg and Matthew J.W. Cock. Global Invasive Species Program, 2001.

Photo: Steve Russell/Toronto Star



Pedestrians in downtown Toronto in a cloud of soybean aphids (*Aphis glycines*), an invasive pest from eastern Asia

National strategies are required to assess the full scope of the threat of invasive non-native species and deal with it effectively. Also critical to success is a mechanism for international co-operation to stop invasions at their source and to foster the sharing of lessons learned in preventing and dealing with invasions.

There are numerous methods available to control exotic species once they have invaded a new territory – mechanical, chemical and biological. Biological control methods include the release of sterile males; microbial pesticides; large scale or inundative release of pathogens, parasitoids or predators; augmentation of existing natural enemies during pest outbreaks; habitat management to enhance levels of natural enemy control; and classical biological control.

The most important method of biological control for management of invasive species is classical biological control. At its simplest, this is the introduction of natural enemies from the original range of the target species into new areas where the pest is invasive.

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Guest Author Cory Lindgren

Invasive Species, Biological Diversity & Biological Control

When I discuss my research interests with friends and family, I can only imagine the images they conjure up. Space aliens, men from Mars, Klingons, Marvin the Martian and the latest National Inquirer report of a three-headed man-eating fish – *these* are invasive alien species??

Invasive alien species have risen to prominence over the past several years, fueled in the USA by President Clinton's 1999 executive order recognizing the seriousness of the issue and promising major program funding. In Canada, the national plan *Addressing the Threat of Invasive Species* (currently in draft form) may fulfill the same function. As the trend towards globalized economies continues, there are increases in both the sheer volume of trade and the number of trading partners. Thus the rate of introduction of invasive alien species into Canada is not likely to decline. Globalization has broken down barriers that previously restricted dispersion. We can expect to see more challenging invasive alien species in the days ahead.

The Convention on Biological Diversity, an international treaty adopted in 1992, reported that *the rate of biodiversity loss is increasing at unprecedented rates* and that introductions of alien species which threaten ecosystems, habitats and species are a contributing factor. While not all invasive alien species are deleterious, some cause economic and ecological damage. It has been estimated that invasive species cost the U.S. economy \$140 billion a year. Ecological impacts include displacement of native species; alteration of ecological processes; and degradation of habitat that provides food, shelter and breeding substrates for wildlife, including species at risk. It is believed that over 40% of listed threatened or endangered species in the U.S. are at risk primarily because of invasive species.

One such species, purple loosestrife (*Lythrum salicaria*), is estimated to invade 115,000 hectares of wetland habitat in the U.S. annually. It is capable of invading natural and aquatic areas, including wetlands that serve as critical breeding habitat for species at risk such as the least bittern (*Ixobrychus exilis*) or yellow rail (*Coturnicops noveboracensis*). In some cases purple loosestrife forms near-monocultures which displace native flora and reduce ecosystem biological diversity. All in all, it is one serious weed.

Many introductions of invasive plants are the result of escapes from gardens into natural areas. Purple loosestrife is a case in point. Despite attention from various levels of government and in the popular media, it is still found in many gardens. Cultivated varieties once thought to be sterile and safe for landscaping have hybridized, further contributing to its spread. Increasing public demand for attractive plants for use in aquascaping and water gardens will likely escalate these kind of exotic introductions.

Biological weed control, a process that attempts to reunite an invasive weed with its natural enemies, provides a mechanism for protecting and enhancing biological diversity from alien species. Classical biological control of purple loosestrife is proving to be one of the great biological control success stories. Beginning in 1992, releases of biocontrol species such as *Galerucella californiensis*, *G. pusilla*, *Hylobius transversovittatus* and *Nanophyes marmoratus* took place in Canada. New provinces and states continue to implement new biological control programs against purple loosestrife. In some cases, biological control agents have resulted in almost 100% reduction in the target weed. *Galerucella californiensis* has been particularly effective in Canada. Researchers are finding that niches once invaded by purple loosestrife are being re-occupied by desirable native species such as sedges and cattail.

Historically, biological control has offered solutions for *agricultural pests*. But purple loosestrife is serving to introduce new "wet" audiences to the science of biological control. The purple loosestrife story is a stellar example of how an invasive alien species can be managed through a classical biological control program, leading to enhanced ecosystem biological diversity. ■

Cory Lindgren is a habitat biologist who researches the impacts of invasive species and the performance of biological control agents against purple loosestrife. He is the Canadian contact for the biological control of purple loosestrife and manager of the Manitoba Purple Loosestrife Project.

For information on the Manitoba Purple Loosestrife Project visit www.purpleloosestrife.org



Galerucella californiensis, an effective
biocontrol agent for purple loosestrife



Agriculture and Agri-Food Canada Agriculture et Agroalimentaire Canada

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Managing the Urge to Splurge

In the development of biocontrol agents, laboratory research is essential for many objectives, such as describing an agent's physiological host range. But the really difficult step, according to Agriculture and Agri-Food Canada's Dr. Robert Bouchier, is when you transfer the agent to the open field. This 'proof of concept' stage, in which the behaviour of the biocontrol agent is assessed in the larger environment, is where the rubber really hits the road or, more appropriately to entomologist Bouchier's work, where the beetle hits the weed.

Bouchier and his colleagues, working out of southern Alberta (Lethbridge), are attempting to control a troublesome weed called 'leafy spurge' (*Euphorbia esula*). The plant produces a sap which is toxic to cattle and reduces grass cover on rangeland in western Canada and the north-central United States. Leafy spurge was imported from Europe in the early 1800s and is now responsible for annual losses of \$130 million to U.S. agriculture alone.

To combat interloper plants such as leafy spurge, biocontrol experts like Bouchier first screen the plant's natural enemies back in Europe, in order to find the one that most effectively controls it without also preying on other plants (i.e., the one that most 'narrowly targets' leafy spurge). They then take steps to establish the plant predator here and work out the best ways of subjecting the target weed to the predator's appetite. Dr. Bouchier's current work is focused on this last or *implementation* step, which involves collaboration with 'field men' supplied by municipalities in the Lethbridge area.

"The agent we use to control leafy spurge here and in the U.S. is a European beetle, *Aphthona lacertosa*," explains Bouchier. "The groundwork host range testing on this and other *Aphthona* species was done by CABI International's Swiss-based centre and approved for use in Canada by the Canadian Food Inspection Agency, the nation's watchdog over introduction of new biocontrol agents." *A. lacertosa* is effective because its larvae kill the leafy spurge root system (it spreads by suckers) and because there are enough adult beetles to defoliate the plant and prevent the spreading of seeds.



While the general concept is simple enough, it turns out that these beetles are a finicky lot, with strong preferences for soil types and climate. This has required Bouchier to set up individual 'nurse' sites throughout the municipalities, the idea being that each of the field men will eventually (in three to five years) have his own special site for beetle collection and redistribution to weed-infested areas. To date, the beetles have been shown to control 100 by 50 metre patches of spurge at multiple locations, but the weed has had a 100-year head start spreading on the landscape.

Bouchier's goal is to distribute the beetles as widely as possible and establish the nurse sites to the point where redistribution of the beetles by the field men will be a routine task. He sees training in beetle biology and site establishment as a major challenge for this kind of approach to weed control. Says Bouchier, "You have to know how to handle these beetles and appreciate the time frame required for them to work – three to five years. One fellow called up to say that he had released the beetles, but after a few weeks hadn't see any change in the spurge. So he sprayed."

Bouchier describes how biocontrol agents are routinely used with other control methods, including herbicide sprays, in integrated pest management (IPM) programs. A recent American modeling study of land treated with *A. lacertosa*, sheep grazing and herbicide sprays indicated that spurge had been reduced to under 50 % of the projected infestation without these controls. Canada/U.S. cooperation on biocontrol has been extensive and successful over the years, employing reciprocal arrangements whereby each country provides agents to the other as needed. The two countries have set up weed biocontrol consortia for specific weeds, with approvals requiring extensive testing of the agent's effects against non-target plants and endorsement by a joint technical advisory group.

It appears that Bouchier's labours are bearing fruit. As a result of his and others' efforts, *Aphthona lacertosa* is home on the range, munching happily on both sides of the border.



Aphthona lacertosa
adults

Vertalec: Makes Aphids Come Unglued



Whitefly adult
infected with
Verticillium lecanii

Despite their innocent appearance, aphids are rather insatiable creatures when considered en masse, which is how they're usually found, congregating under a tomato leaf in all their sugary splendour. Their ability to short-circuit time-consuming pregnancies by being essentially born pregnant means that aphid populations can 'explode' and quickly outflank the predations of their enemies. The worst part is that aphids transmit some truly nasty plant diseases. The best medicine for aphid attacks is preventive - you've got to manage them early before they eat you out of house and home.

Aphids are common pests on nearly all indoor and outdoor ornamental plants, as well as vegetables, field crops, and fruit trees. They feed by drawing sap from plant tissue, using mouthparts adapted to piercing and sucking. Light infestations are usually not harmful, but higher populations can cause a variety of damages. Some aphids also act as vectors of plant disease during the feeding process. The green peach aphid, one of the most common aphid pests in Canada, is capable of transmitting over 100 plant viruses.

Many aphid species are perfect examples of now-established pests having begun life in North America as "invasive species". A number of aphid species arrived with early horticultural imports from Europe, while some appear to have migrated from East Asia. Because aphids are predominantly northern species, there continue to be accidental introductions into southern nations such as New Zealand and Australia, introductions which cause concern because of their potential impact on the environment and biodiversity. Nevertheless, there have been no attempts to eradicate any aphid species after its accidental introduction into any country. Such an undertaking would be extremely difficult. The aphid's ability to rapidly colonize a new area is a reflection of their small size, ability to quickly reproduce asexually and in great numbers, and the capacity of winged forms to fly or be blown large distances.

Aphid infestations have usually been managed with a variety of insecticides, including organophosphates and synthetic pyrethroids. But many aphid pests are developing resistance to a variety of insecticides.

Enter Vertalec, a commercial microbial insecticide based on a lowly fungus. Vertalec is one brand name for a formulation of the fungus known scientifically as *Verticillium* (= *Lecanicillium*) *lecanii*. It's manufactured by Koppert, a company based in the Netherlands with operations in Canada and many other countries. When Vertalec is sprayed on infested plants, the fungi germinate and produce thread-like hyphae which penetrate aphid bodies and proliferate, destroying tissues, growing through the insect cuticle, and killing the pest within 5-8 days. In one test, a single application of Vertalec provided control of the green peach aphid on greenhouse chrysanthemums for three months.

Vertalec is effective against a wide variety of aphids, including the green peach (*Myzus persicae*) and melon cotton aphid (*Aphis gossypii*), perhaps the most serious aphid pests in Canada. It's registered in several European countries and Japan for use on vegetable, ornamental and legume crops. Depending on the crop, it's used at a rate of 1000 to 2000 litres per hectare.

Vertalec has the important property of being compatible with most parasitic and predatory arthropods. Even though it can kill immature *Encarsia formosa* which parasitize greenhouse whitefly, in application, the combination of the two natural enemies is better than either alone. As a result, Vertalec can be readily incorporated into integrated pest management programs that utilize other biological control agents.

Though the product is not registered in Canada as yet, both Koppert and Canadian growers are interested in pursuing registration. The mostly likely use pattern would see the product provide control of green peach aphid and melon cotton aphid on greenhouse chrysanthemums and peppers. ■

Control for Lawn Grubs

KeeP lawn grubs under control with beneficial nematodes

It's becoming the newest Canadian spring ritual. After dusting off the lawn mower, hauling out the lawn chairs and unwrapping the barbecue, Canadian homeowners now need to check their lawns for grub damage. The prime suspects are the immature stages of several insects, including the European chafer, European crane fly, and Japanese beetle (all species native to other continents), which damage turf by chewing on its roots. In mild cases, the grubs will only thin turf. In heavy infestations, lawns can be totally destroyed in 2-3 weeks, especially when skunks, raccoons, moles and birds tear up sod to feed on the little critters. Repairs involve stripping the affected area, adding appropriate soil and seeding or sodding. The damage runs from \$500 - \$2000 for a typical lawn.

The European chafer (*Rhizotrogus majalis*) was first reported in the Eastern U.S. in 1940. The pest is believed to have hitchhiked on plants shipped from Europe in the 1920s. By 2001, it had migrated as far as coastal British Columbia. And, like other imported pests, there are no native predators, parasites or diseases in North America which provide adequate control.

Typically, chafer management has relied on organophosphate insecticides. But many of these are being phased out and homeowners and landscape professionals are searching for safer, biological solutions. Products based on nematodes are increasing in number in the marketplace and may provide a solution.

Nematodes, essentially microscopic worms, work by parasitizing the grubs, i.e., penetrating the body of the grub and laying eggs. Once inside, the nematodes release bacteria into the insect's body and toxins released by the bacteria kill the chafers within a few days. Three species of nematodes appear to be particularly effective at managing grubs. Their scientific names are *Steinernema carpocapsae*, *Heterorhabditis bacteriophora* and *H. marilatus*. Product names include Lawn Guardian, Scanmask and Hortscan.

A number of scientific researchers have conducted controlled experiments which test the efficacy of nematode products. Results have been mixed. But, on the ground, some lawn and landscape companies have had very good success. Scott Cockwell, director of Safe Lawn Care in Ottawa, has been working with nematodes for seven years. "In 2004 we did close to 1000 applications. In the fall, we had only four callbacks about grubs and all involved rodents picking at the grass. Further evaluation showed grubs in low numbers and no visible turf damage other than that caused by the rodents. In my opinion, nematodes work amazingly well. I see proof each and every season."

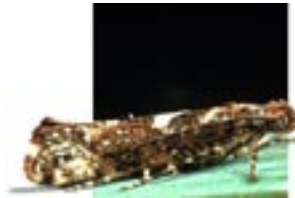
The cost of treatment is low and, equipped with a little knowledge, homeowners can buy and apply the nematodes themselves. A do-it-yourself application costs about \$30-35 for a 2-3,000 square foot lawn, with professional applications running \$85 and up. This isn't about eradication, says Cockwell. "Grubs are now a natural part of lawn ecology. The trick is to keep their numbers below the point at which they damage turf, which is about five per square metre for European chafer." ■



Mature European chafer grubs (*Rhizotrogus majalis*), shown actual size

On the “Leekout” ...

For a Biologically-based Pest Solution



*Acrolepiopsis
assectella*, the
leek moth

Leek moth (*Acrolepiopsis assectella*) is a native European pest of *Allium* crops such as leek, garlic and onion. It was first discovered in Canada in 1993 and by 2000 had found its way into garlic crops near Ottawa. From there, it has spread further into eastern Ontario and southwestern Quebec, Canada's hub for *Allium* production. The moths are capable of flying short distances between fields and may fly en masse to new locations. Experience in northern Europe suggests that the pest may spread, albeit slowly, throughout Canada.

Leek moths can do considerable damage to their favourite crops. For example, after hatching on leek leaves, young larvae mine the leaves and move down into the stalk as they mature, often rendering the crop unmarketable. Populations build slowly in the spring, causing little or no effect on early crops. But in areas with longer growing seasons, the pest can cycle through several generations in a year and damage is much more serious. In Italy, for instance, yield loss in leeks can reach 40% in late summer.

While leek moth has not yet infiltrated the larger *Allium* growing operations in Canada, the industry it threatens is of considerable importance to a number of provinces. In 2001, Canadian *Allium* crops were worth over \$75 million, with approximately 80% of production occurring in southern Ontario and Quebec. Generally speaking, the moth is well controlled in conventional production by insecticides which are applied for the control of other pests. But organic producers in infested areas face substantial crop loss unless measures are taken to develop biological control.

In response to this new threat to cultivated *Alliums*, not to mention wild *Allium* species, Agriculture and Agri-Food Canada with support from its Pest Management Centre has initiated a programme to develop sustainable approaches to managing the leek moth.

A critical part of the initiative is a review of the feasibility of classical biological control. This will involve searching for a European parasitoid species that contributes to the low leek moth densities observed in many regions of Europe. Though many European leek moth parasitoids have been described, there is insufficient knowledge of their community structure and their ability to manage moth populations.

To date there are no known examples of an organized release of an insect biological control agent against leek moth. Rather, pesticides are the traditional solution to high leek moth densities in Europe. At present, there are no registered pest control products in Canada for leek moth. The identification, evaluation and release of a successful classical biological control agent would inevitably benefit the entire *Allium* growing industry by reducing the population and the spread of the leek moth.

The work on biocontrol is proceeding within the framework of an integrated programme for control of the leek moth. Other components of the research programme include developing a degree-day model to predict when the pest is most vulnerable and evaluating microbial biocontrol agents for application as sprays. ■

By Wade Jenner (Carleton University) and Peter G. Mason (Agriculture and Agri-Food Canada)



“That’s the trouble with the older generation—they’re too intolerant.”

Pheromones: An Early Warning System

At the height of the Cold War in the 1950s, a necklace of radar stations was strung across the top of Canada. This DEW line (Distant Early Warning) was installed in order to deter the threat of nuclear attack and defend a continent from invasion. Could the same principle defend against invasive species? Is there an early warning system which could alert us to invasions from insects and plants which may pose serious threats to the vitality, biodiversity and stability of forests and crops in Canada and elsewhere?

Perhaps we could learn a lesson from 'down under'. Australia has adopted a simple three-step biosecurity strategy which they believe will protect their valued resources from invasive species for decades to come. First, they take an inventory of their natural resources and those of their trading partners. Second, based on this information, they identify the species which have the potential to be introduced and to be highly damaging. Finally, and most germane to the subject of this article, they attempt to develop pheromone-based detection programs for these species.

Pheromones are chemicals secreted in minute amounts by an organism in order to elicit a particular reaction from another individual of the same species. For example, many female insects produce pheromones which attract males; this is the basis for much of pheromone-based detection. In the past, detecting the presence of invasive species has been like looking for a needle in the proverbial haystack: a tedious search through giant ships for egg masses, and through farms, orchards, forests, and backyards in an attempt to visually locate the species in question. On the other hand, pheromone-baited traps bring the invasive species to the researcher, rather than the other way around. An easier, less time-consuming, less expensive and much more effective early warning system.

Dr. Gerhard Gries is an insect communication ecologist at Simon Fraser University in Burnaby, B.C. With his colleague Dr. Paul Schaefer (U.S. Department of Agriculture) and others, Gries has identified and analyzed the components of a number of insect pheromones. This research has allowed them to develop pheromone-based monitoring systems which can be used to detect invasive forest and agricultural pest insects. Many of the pheromones have been identified in lymantriid moths, including the nun moth (*L. monacha*), casuarina moth (*L. xylina*) and pink gypsy moth (*L. mathura*).

In 1996, the white-spotted tussock moth (*Orgyia thyellina*) was discovered in suburban Auckland, New Zealand. The New Zealand government, hearing of Gries' work with lymantriids and pheromones, asked for his assistance. Gries' hard work was about to pay off.

If left unchecked in New Zealand, it was believed that the white-spotted tussock moth would have spread throughout the country in less than a decade, a scenario with massive environmental, trade and health implications. The moth had the potential to damage parkland, private gardens and the willow trees used extensively in New Zealand for shelter, soil and water conservation. Exports from New Zealand may even have been restricted, based on the moth's presence in the country.

A two-year program of eradication was implemented. The first year featured ground and aerial spraying of the bio-insecticide *Bacillus thuringiensis kurstaki* (*Btk*). In the second year, Gries' work on pheromones came to the fore. In an effort to monitor moth populations after the spray campaign (and thereby the success of the program), the tussock moth's pheromone, identified by Gries and his colleagues, was placed in 7500 traps across the city of Auckland. Not a single moth was captured. The programme ended in June 1998, having successfully eradicated the pest from the country. A follow-up pheromone-based detection effort in 1999 also did not turn up a single moth.

Canada certainly has its share of problems with invasive species. The gypsy moth (*Lymantria dispar*) and its relatives rank near the top of Canada's most unwanted list. Larvae of the gypsy moth and other lymantriid moths are forest defoliators. Trees are not directly killed, but are weakened and their growth retarded. More than 20 eradication campaigns have been carried out in British Columbia's lower Fraser Valley and on southern Vancouver Island over the last 25 years against the gypsy moth, using *Btk*. The European strain of gypsy moth has damaged Eastern North American forests for over five decades. One study estimated that total economic losses from gypsy moths in Pennsylvania between 1969 and 1987 totalled \$219 million. By 2000, gypsy moth infestations ranged from New Brunswick and Nova Scotia to Lake Superior.

While there have been biocontrol successes in Canada, there is a need for a proactive and systematic approach. Such a program would serve to protect our natural ecosystems and the sustainability of agricultural and forest industries from the devastating impact of invasive exotic insects. ■



Larvae of the
gypsy moth
(*Lymantria dispar*)

Books

K. M. Heinz, R. G. Van Driesche and M. P. Parrella (eds.) 2004. *Biocontrol in Protected Culture*. Ball Publishing, Batavia, IL. 552 pp.

This book is a comprehensive overview of the challenges of providing biological control solutions for arthropod pest problems in greenhouse and shaded structure crops. Among the topics covered are the prerequisites for a successful program, working with the suppliers of natural enemies, practical aspects of sampling and management of pesticides, biological control of specific pests, current implementation programs and the future of biological control-based pest management systems. This book, which takes a global view in terms of geographic location, expertise and perspective, is targeted for agricultural professionals, but should also be very useful for researchers and students in biological control or IPM.

Conferences/workshops

International Workshop on Invasive Plants in the Mediterranean Regions of the World, Montpellier, France, May 25-27, 2005.
Contact: S. Brunel, Cons. Bot. Natl. Med. de Porquerolles, 63 rue Auguste Broussonnet, 34090 Montpellier, France.
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Phone: 33-0-49-923-2214.
Web: <http://www.ame-lr.org/workshop>

Canadian Phytopathological Society Annual Meeting, Edmonton, Alberta, Canada, June 14-18, 2005.
Contact: D.A. Gaudet, Ag. & Ag-Food Canada, Box 3000, Research Station, Lethbridge, Alberta, Canada.
E-mail: GaudetD@agr.gc.ca.
Phone: 1-403-317-2278.
Fax: 1-403-382-3156.
Web: <http://www.cps-scp.ca/meetings.htm>.

Symposium: Impact of Exotic Invasive Plant Species on the Forest Ecosystem (during 22nd IUFRO World Congress) Brisbane, Australia, August 12th, 2005 (tentative date)
Contact: R.K. Kohli, Ctr. for Environment, Panjab Univ., Chandigarh 160 014, India.
E-mail: RKKohli45@yahoo.com
Phone: 91-172-253-4015.

Erratum: In issue #1, the photo of *Gymnetron antirrhini* on page 2 was placed there in error. This species attacks toadflax and was accidentally introduced in 1957. The species that was introduced in 1951 and should be in the photo is *Chrysolina hyperici*, released against St John's Wort. The website version of issue #1 has been corrected.

Invasive pest Asian Longhorned Beetle (*Anoplophora glabripennis*)

Are Invasive Species Born Bad?

One key question for ecologists is what makes invasive species so invasive. Do certain species simply have an innate potential to grow and reproduce rapidly? Or does invasiveness result from evolutionary changes that occur after an introduction? As ecologist Kristina Schierenbeck of California State University in Chico puts it, "Are invasive species 'born' or 'made'?"

Most ecologists have long assumed that invasiveness is just a matter of being in a favourable environment. If an organism introduced into a new region leaves behind its natural predators, competitors, and parasites, its chances of reproductive success increase. Recently, however, ecologists have explored whether species may also evolve to become invasive in their new homes. This "evolution of increased competitive ability" (EICA) hypothesis, proposed in 1995 by ecologists Bernd Blossey and Rolf Nötzold, is just now being tested rigorously.

There are some "very compelling examples and evidence that EICA can occur," says ecologist Dana Blumenthal of the U.S.D.A. Agricultural Research Service in Fort Collins, Colorado. But "the jury is still definitely out" on the extent of the phenomenon, he adds. The EICA hypothesis predicts that once an organism escapes its natural enemies, it no longer needs the defenses it had evolved against them. If these defenses use up precious energy or resources, natural selection should favour the organism investing instead in traits that give it a competitive edge over its new neighbors. For a plant, this could mean larger size, faster growth, or greater reproductive capacity, all adding to its invasive nature.

Evidence for EICA was offered by Evan Siemann and William Rogers of Rice University in Houston, Texas, who work with the Chinese tallow tree, *Sapium sebiferum*. They found that trees from introduced southern U.S. populations show faster growth and reduced investment in chemicals that defend against leaf-eating insects compared with trees from native Asian populations. As with most EICA studies, the work featured "common garden experiments," in which native and introduced plants are grown side by side to control for environmental variables. The investigators found that Asian trees outperform American trees in settings with native Asian herbivorous insects, whereas American trees outperform Asian ones in settings without these insects. Many scientists, Blumenthal says, consider this evidence the strongest so far in support of the EICA hypothesis.

However, a study of the European plant garlic mustard, *Alliaria petiolata*, which arrived in North America 150 years ago, failed to support the hypothesis. Experiments presented by Oliver Bossdorf of the UFZ Centre for Environmental Research in

Halle, Germany, and colleagues did show that American populations had lost their resistance to a European weevil that specializes on the plant. But when the group then grew American and European populations in side-by-side competition, plants from native European populations outgrew those from introduced American populations.

Perhaps the most extensive common garden experiments thus far involve St. John's wort, *Hypericum perforatum*, the plant of alternative medicine fame, which was introduced from Europe to America two centuries ago. Ecologist John Maron of the University of Montana, Missoula, and his colleagues collected seeds from 50 St. John's wort populations across Europe and North America and then grew European and American plants in common gardens on both continents. Maron's group then measured levels of three chemicals the plants make to deter insects. The American plants exhibited lower levels of the chemicals, indicating they had lost defenses since their introduction. When grown in Europe, the American plants also suffered more infection and mortality than the natives, revealing that the apparently weakened defenses did have a real effect.

Did the American plants that saved on defense invest their new gains into competitive ability, as the EICA hypothesis predicts? Apparently not. The American plants showed no trend toward larger size or greater reproductive ability when growing in the United States.

Maron's work tested EICA more comprehensively than any previous study, according to some ecologists. "He did exactly the experiments that needed to be done," says Marc Johnson of the University of Toronto. Maron doesn't perceive his results or those of Bossdorf's group as undermining EICA, however. He says that circumstances will vary for every species. In a recent meeting, both Blossey and Blumenthal summarized previous tests of the EICA hypothesis and found that of 14 studies, five supported EICA, one rejected it, and the remainder were inconclusive. "One flaw of EICA," says ecologist Peter Kotanen of the University of Toronto, "is that it envisions a very simple trade-off between defense and growth. The real world is more complicated."

Nonetheless, the ongoing rigorous assessment of the hypothesis demonstrates that the study of invasive species has come of age. "What I found striking ... is how much invasion biology has matured," says Kotanen. "We've gone from case histories and compilations to people finally doing experiments, and we've probably learned more in the last 10 years than in the five decades before." ■

Adapted from Jay Withgott's article in Science, August 20, 2004

