RECONSTRUCTING AN ECOSYSTEM: A THEORY UNIFYING INVASION BIOLOGY AND BIOLOGICAL CONTROL

Tom BELLOWS

Department of Entomology, University of California
Riverside, CA 92521 U.S.A.

bellows@ucr.edu

ABSTRACT

Invasion biology is centered around two focusing themes – (i) will an invasion result in an establishment, and (ii) does the establishment of a new species result in a threat to existing species or critical community or ecosystem characteristics. In biological control, we are continually faced with two different types of invasions. The first of these is the unintentional (or sometimes intentional!) invasion of a plant or animal species into a new area. The second type is the subsequent, and intentional, invasion of natural enemies introduced for the purpose of ameliorating the negative effects of some previously invasive species that has become a threat to other species or to some characteristic of the invaded ecosystem. This paper presents a theory of interactions, based on both guild structures in a community and on population dynamics, that brings together these two types of invasions and connects invasion biology and biological control. In essence, the connections between these two different types of invasion share common population dynamic structure, and a common guild structure. However, the impact on the ecosystem in which these invasions takes place is vastly different between the unintentional introduction of a damaging species compared with the introduction of a species in a higher trophic level. The theory is presented in both ecosystem structure form and in the form of a model of the population dynamic processes involved. The model outcomes are related to current issues and recent projects in biological control.

INTRODUCTION

First, I would like to express my thanks to the symposium organizers for all their hard work putting together such a wonderful meeting, and secondly I would like to thank them for the opportunity of addressing this august body about some ideas I have relating ecosystem or community disturbance and biological control.

I am strongly of the opinion that biological control is the most powerful ally that a disturbed ecosystem has in the efforts to return it to ecological health. In this paper I will try to demonstrate why I think that this is so by following a path from simple ideas to more complex ones in order to demonstrate the power that biological control may have in helping manage ecosystems at risk from invading species. The path I will take is this: I will look at what happens in nature in biological control programs. I will then show that we can capture what happens in nature in a simple model of population dynamics. Then I will expand the

model to include migration in four different types of ecosystems. In these ecosystems, I will simulate the invasion of a species and its remedy through the introduction of a natural enemy. And in these cases, we find the same power and results in a complex ecosystem as we do in the simpler, two-species cases.

MATERIALS AND METHODS

To develop these themes about biological control and ecosystem-wide biology, I am going to draw upon real-world data to first give us an impression of what biological control of arthropods can do in terms of population suppression (Van Driesche & Bellows 1996). Of the some 1200 biological control programs developed against arthropods and other pests, there is relatively little data on what we would consider modern quantitative population dynamics. Early qualitative reports of biological control success were exuberant about their impact. More recently, we can find in the literature (and in our own work) quantitative studies on the impact of natural enemies on harmful invasive species.

Fig.1 shows a few examples of the impact of introducing a natural enemy into an already established population of a harmful or pest species. In every case we find important and repeated characteristics. Although the figure only indicates three examples, we find throughout the quantitative literature four features common to such programs. One, that whenever an arthropod species invades a new territory in which it can survive and reproduce well, its population grows to a size that occupies all the available resource that is critical for that species (such as leaf area, for example). Second, we find that when an effective natural enemy is introduced, it requires some 10-15 generations for the population of the natural enemy to catch up to the pest species density and exert a sufficient force on it that the pest population collapse. Third, we see that in a biological control program, once the natural enemy's population density has caught up with the pest, the pest population crashes to phenomenally low densities, typically 4-8 orders of magnitude lower than prior to the natural enemy's introduction, a control level unsurpassed by any other mechanism or pest control known. The final feature of this control is that it appears permanent. The pest and natural enemies continue to exist at very, very low densities without disruptions or outbreaks.

These four characteristics of biological control programs and their impact on pest species appear pervasive, and many examples can be found from the biological control of pests in many different environments. This pervasiveness implies that there are intrinsic features of pest-natural enemy systems that are found across many taxa, in many different environments. So a task is set before us to uncover, or at least mimic, what some of these features are, so that we might come closer to an understanding of what makes biological control so powerful in so many different settings. As a beginning, I will present a graphical view of what happens to an ecosystem when it suffers an invasion of a harmful species.
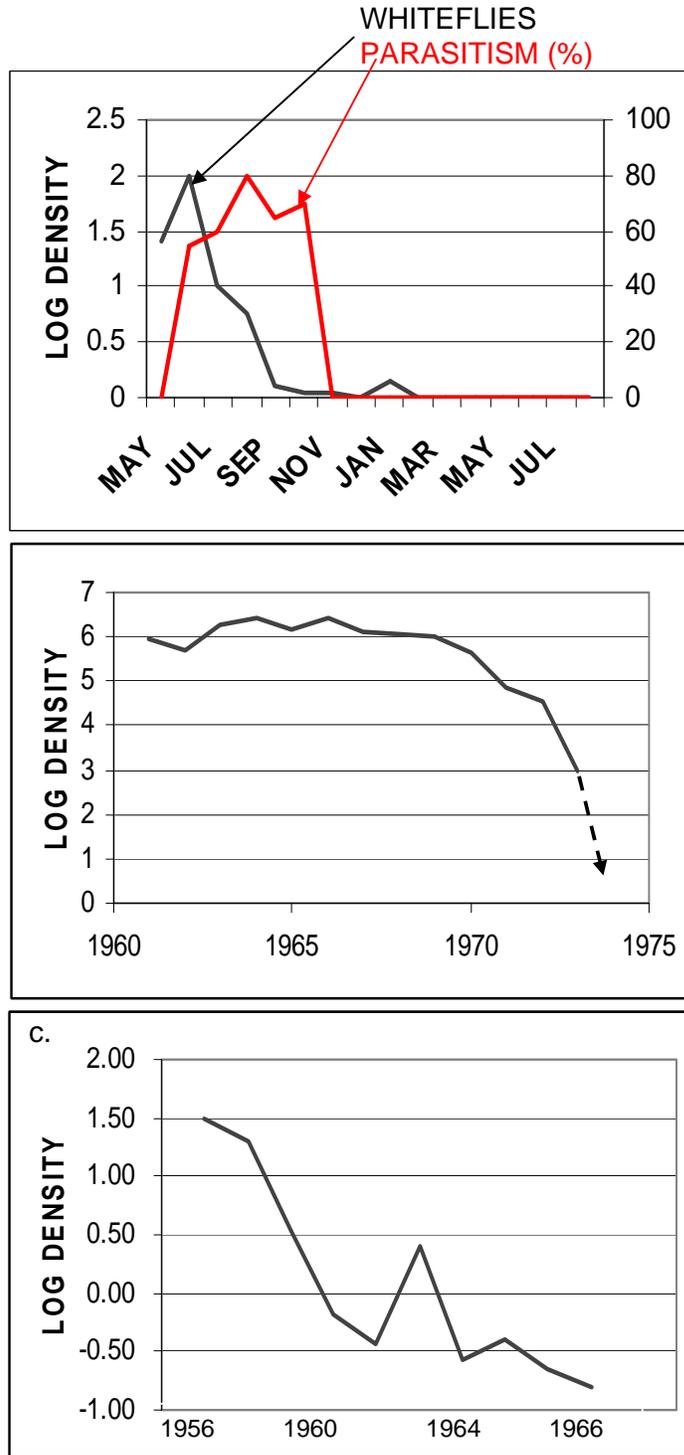
Figure 1. Three examples of biological control outcomes that emphasize the four important points of biological control: first, that an invasive species can reach phenomenal densities. Second, biological control can bring about major suppression of target pest. Third, an expectation that it will take 10 to 15 generations to achieve such suppression, and fourth, that such suppression is permanent. (a), giant whitefly, Bellows unpublished; (b) larch sawfly after Ives 1976; (c), olive scale, after Huffaker 1971.
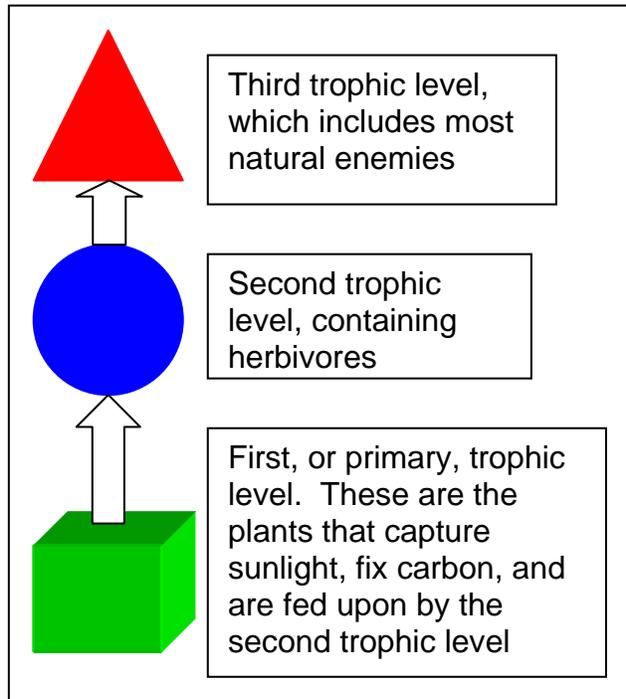
4

Third trophic level, which includes most natural enemies

Second trophic level, containing herbivores

First, or primary, trophic level. These are the plants that capture sunlight, fix carbon, and are fed upon by the second trophic level

Figure 2. A fundamental community consists of plant species, herbivore species, and predator or parasitic species.
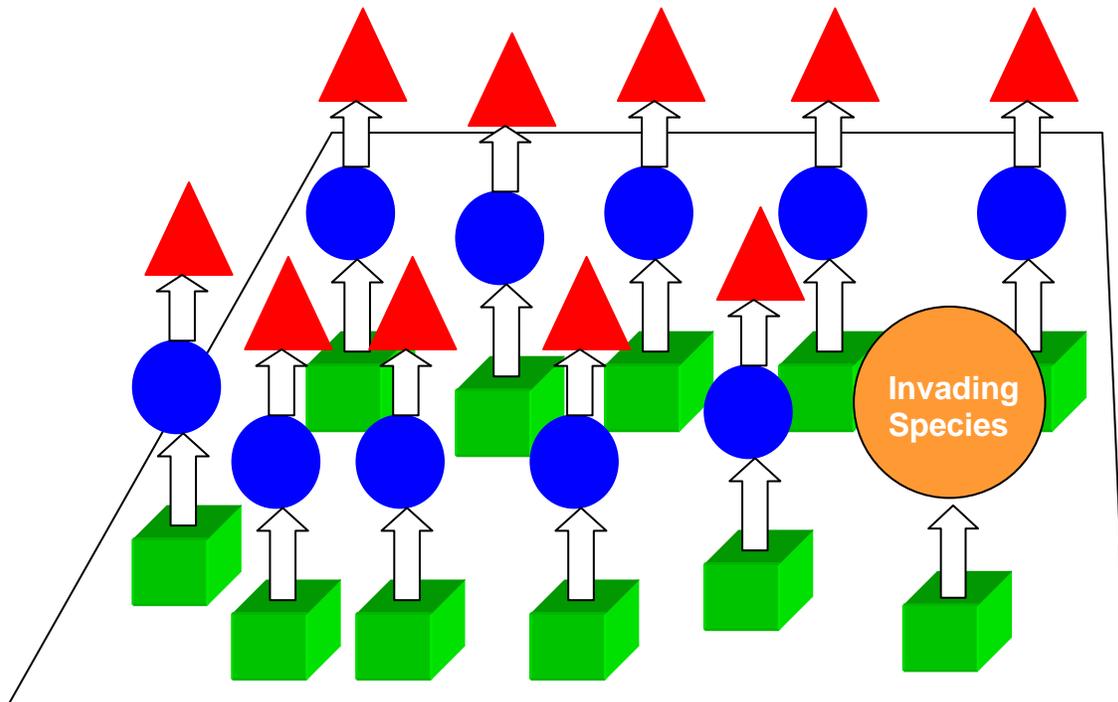
Invading Species

Figure 3. An ecosystem is composed of many communities operating together in the same space and time. One community may be present in many numbers. There also may be many different communities that interact with one another. An invasion by a species not a member of the ecosystem may reek havoc on ecosystem function.

In Fig. 2 I have characterized the structure and function of a simple, three-species community. Having many such communities, and mixing them with similar communities made up of different species (Fig. 3), provides the basis for an ecosystem in dynamic homeostasis. A major problem arises when a species new to the ecosystem, an invading species, arrives and begins to grow out of control, using up nutrients, or competing for foliage, and changing the homeostasis to the point that the ecosystem can no longer function as is had.

We now need a tool, or a model, that captures the four essential features of a successful biological control campaign. The structure of such models has been the object of much study, from the initial work of Thompson (1924) and Nicholson and Bailey (1933), through to the present day. The simplest and most appropriate form is a pair of difference equations, as shown here:

$$h(t+1) = F \bullet h(t) \bullet g(h(t) \bullet f[h(t),p(t)]$$

$$p(t+1) = h(t) \bullet g(h(t) \bullet \{1 - f[h(t),p(t)]\}$$

A bit of explanation makes these equations very simple to follow. The herbivore population that is the target of a biological control program is represented by 'h'. The value of t is the generation in which the equations are operating, and is iterated or added to each time we use the equations. The symbol F represents the fecundity of the herbivore. Now we have only the functions g and f to deal with. At extremely high densities, the herbivore may run out of resources necessary for optimal reproduction. So the function g(h) is simply the proportion of offspring that survive in that generation due to any limit placed on the population by lack of resources. The function f(g,p) tells us the proportion of herbivores that escape parasitism, and hence go on to survive to the adult stage and produce the generation h(t+1). The proportion that does not escape parasitism (in the second equation) eventually become parasitoid adults, p(t+1), in the next generation. This pattern repeats itself over and over, generation after generation.

I will not bore you with nearly a hundred years of research trying to find functions for g and f that actually describe what we see in biology and in biological control situations. Suffice to say that, after many trials, two have come to be recognized as the most suitable functions. For density dependence in the herbivore population, a model with the necessary properties was provided by Maynard Smith and Slatkin in 1973 (Bellows 1981), where

$$g(h) = 1 / (1 + (ah)^b)$$

In this model the parameter a is simply a scaling parameter, helping to fix the equilibrium density of the herbivore population in the absence of any predation or parasitism. The parameter b has bearing on the degree of severity of the density dependence in the herbivore populations. In most insect populations, density dependence found in nature is mild (Bellows 1981), and in all the simulations reported here b has the value 1, which represents simple contest competition. The parameter a was given the value 0.001 for every location, and the fecundity (F), that is, the number of offspring that do not perish due to density independent causes, was assigned the value 4. This provides an equilibrium herbivore density, in each location (and in the absence of parasitism), of 3000 individuals.

Of the many models employed by many authors for predation or parasitism (function f(h,p)), only one has emerged that can demonstrate the properties we see in nature: major suppression of an invading species, with stable, continuing populations (May and Hassell 1988). This model employs the negative binomial distribution of attacks by a natural enemy, that is, the attacks tend to be clumped or aggregated (as are also many herbivorous insects in nature). The function takes the form:

$$f(h,p) = (1 + (a'P)/k)^{-k}$$

The parameter *a'* represents the search efficiency of a single female parasitoid, and the parameter *k* indicates the degree of aggregation of her attacks. In the simulations reported here, these parameters were given values of 0.1 and 0.5, respectively, indicating a moderately efficient natural enemy with a mild degree of aggregation in her attacks.

Before continuing to explore the simulations of ecosystem-level invasions, we must first determine if the tool, that is, the model, is an effective mimic of what we see in natural invasions followed by a biological control program. In order to do so, I ran simulations of just an isolated pair of populations, one herbivore and one parasitoid. Each simulation ran for 20 generations with only the herbivore. At that time, a single natural enemy was added to the population, which was then run for an additional 15 generations. The outcomes are discussed in the Results section, but suffice to say here that they were in keeping with expectations, and validated the use of the model as a tool to explore more complicated ecosystem-level invasions.

6

In exploring the potential ecosystem-level impact of a natural enemy working against an invasive species, there are several significant questions to explore. One is to what degree is the invaded species suppressed when it is capable of movement from one part of an ecosystem to another. Another important issue is whether any suppression achieved is stable, or is subject to erratic fluctuations.

In order to explore these issues, I developed a model of an ecosystem which consisted of 400 locations, each adjacent to two or more locations, placed on a square grid of 20 rows and 20 columns (Fig. 5). Each location was characterized by a parameter ã, which was varied in different ways in the four ecosystems. The parameter ã varied from 0 to 1, and was used to characterize the suitability of each location for herbivore reproduction. The parameter ã was multiplied into the herbivore reproduction equation:

$$h(t+1) = ã•F•h(t)•g(h(t)•f[h(t),p(t)]$$

A location with a value of 1 is highly suitable, and imposes no limit on the herbivore. A location with a lower value of ã would limit the potential reproduction of the herbivore.

Using this model ecosystem I investigated four different patterns for the value of the parameter ã, to represent four different types of ecosystems. In one simulation, all locations in the environment had a value of 1. This, in a way, was the most basic evaluation of the behavior of biological control over a wide, uniform area. In the second simulation type, I placed values of 1 in a regular pattern over the ecosystem, separated by values of 0 (Fig. 5). This might be viewed as representing an orchard, or an urban ecosystem, with each house and yard separated by streets or avenues. In the third simulation, I assigned each location in the

ecosystem a random number between 0 and 1. This is the most diverse and complex system (Fig. 6). In the fourth case, I placed specific areas on the ecosystem map in which the locations had high values of ã, separated by locations with values of 0. This represents an ecosystem with certain vulnerable habitats, in which conditions allow the invading species to flourish, surrounded by areas where the invading species can not reproduce.

Migration in the ecosystem was handled simply, and in keeping with most of what we know about movement in arthropod populations. The premise I followed was as follows: most offspring tend to stay close to their area of birth and rearing (close at least in the sense of the perceived size of the grid). Hence after herbivore reproduction and parasitism, there was a migration phase in which only half of the surviving individuals in a location remained there. Of the other half, 80% were distributed equally in the locations surrounding the one of their birth, indicating moderate amounts of migration. The remaining 10% were considered "far migrators", and were distributed evenly over the entire ecosystem, into locations from the farthest to the closest to where they were born.

RESULTS

TWO SPECIES, SINGLE LOCATION MODEL

Validating a tool such as a model for use in exploring the potential impact of an invading species requires that we examine the behavior of the model in its simplest possible form, and compare the model outcomes with what we know occurs in nature. If the model passes such a test, then it may be useful to generate hypotheses about what may happen in a larger context, that is, in our study what may happen in an ecosystem. Of course, if the model cannot capture the essentials of natural populations, it is an untrustworthy tool and another one must be sought for use in its place.

Of the four essential and common features of an invading species, a biological control program, and the impact on the two populations involved, we can examine each one in turn after conducting simulation studies with the proposed model. I conducted several such studies, with varying values for the parasitoid search parameters and the herbivores growth parameters. One such simulation study, the results of which were typical of all the trials I ran, is shown in Fig. 4.

In this study, we see the rapid rise in density of the invading species, reaching its carrying capacity in just 5 generations. This is equivalent to the invading species occupying all the available resources, as is common when a species is adventive to an area and has no effective natural enemies. In the absence of natural enemies, it rapidly reaches the environmental limit of its growth, and the population is limited by its own density dependence. Here, the model mimics the first of the four common features of a biological control program.

In generation 18, when the invaded species had reached its equilibrium density of 3000 individuals, 10 parasitoids were added to the system. These parasitoids amounted to 0.3% of the host population. But such is often the case in biological control – by the time a natural enemy has been located, screened for safety, and rearing has begun, the invaded species which is its target has been reproducing without limit for many generations. So the entry of 10 adult
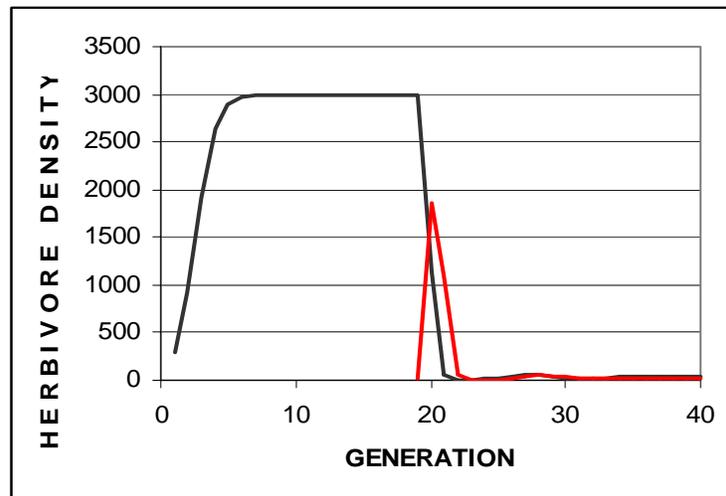
7

Figure 4. A typical simulation run of the model for an invading herbivorous species (black) followed by the introduction of a natural enemy (red) at generation 18.

parasitoids into the system is typical of such programs. As the impact of 10 natural enemies on a population of 3000 herbivores is nearly undetectable, these releases are often referred to as "inoculation" releases, with the expectation that their offspring will start a population growth that will eventually catch up to, and then control, the invading species.

In natural systems where such data are available, approximately 10-15 generations pass before the density of the invader begins to decline, and when it does so, it does so very rapidly. If a sample is taken at the right time, one can often find a leaf covered with the invading herbivore, together with very large numbers of the natural enemy. Here the model appears to be slightly more efficient than what data we have on such matters, bringing the invaded species density down dramatically within five generations.

The last two matters, the degree of suppression and the stability of that suppression, we also see in the modeled populations. The average density of the invaded species after the suppression (generations 36-40) is 31.2, a drop of two orders of magnitude below its previous high level. The standard deviation of this mean population level is 0.95, which is 3% of the mean, and indicates a very stable population. Clearly the impact of the natural enemy in the model has given us an appropriate decline in density, and maintains it with considerable stability.

Note the major drop in density of the invaded species, followed by a moderately stable and consistently low density of both the herbivore and its natural enemy.

ECOSYSTEM SIMULATIONS

Having concluded an evaluation of the model in its simplest setting, we have found that it does have the characteristics and behavior that we see in nature. This does not make the model "correct" in any context – a model is simply an abstract representation a dynamic process. But the fact that the model does capture the dynamical behavior we see among natural populations does give some confidence that we can now apply the model to a wider

scope, and use it to ask questions about the behavior of similar systems, such as an ecosystem which we envisage as a collection of communities each behaving in the manners that the model has been able to replicate. So here we are using the model to explore possibilities, create hypotheses; but we are not attempting to prove something. Hypotheses only get tested by using biological data, and the most useful and related thing a model does is help us create sensible hypotheses to test.

Such testing is beyond the scope of this paper, but we can examine what the model behavior is in the ecosystems that I have proposed testing. Two of these are somewhat trivial, and I will present them *de novo* at the symposium. Two others will suffice to demonstrate what new insight might be awaiting us in the continued study of ecosystems affected by invasive organisms.

The first of these (Fig. 5) represents an ecosystem that has areas suitable for the reproduction of the invading species, separated by regions that are not. Some have termed such a layout an "orchard" model of an agricultural ecosystem (to distinguish it from monocultural agricultural regions). One of the first things we would expect is that the equilibrium density of the invading species should be lower here than in an ecosystem that was uniformly suitable for reproduction, as there is less resource in this ecosystem. Such turns out to be the case, and the equilibrium density for an invading species in this ecosystem is only 36% that of when it is growing in a uniform ecosystem.

Turning to our four expectations from biological control systems, we see that in the absence of natural enemies, the invading species does reach the carrying capacity of this environment quickly. We also note that the population density of the pest falls rapidly following the introduction of the natural enemy, in this case in approximately 7 generations (but this was also the case for this model when evaluated in the simplest trial). The pest population is reduced, and appears to be low and stable for many generations. However, a closer quantitative look shows that the average population density of the invaded species in only 1.5 orders of magnitude lower that its carrying capacity. The standard error of the mean is very low (3% of the mean density), so the new stasis appears very stable. But it does appear that the model does not predict as great a population density reduction as we have seen in many field studies.

Lastly, we turn to an ecosystem that is rather like an abandoned field, or a heterogenous forest, or any other kind of ecosystem that has great variation in its resources over the space it occupies. The average value of the parameter ã in this ecosystem is 0.500, thus we might expect that the carrying capacity of the ecosystem would only be half of what we would find in an ecosystem that was uniformly suitable for an invading species. This is indeed the case. But let us turn to our four characteristics and evaluate what the model says about biological control as a tactic in such a diverse system.

We find that an invaded species does indeed climb to the overall carrying capacity very quickly. When the natural enemy is introduced, a new stasis is reached in approximately 10 generations, fitting well with what we see in nature. However, the new equilibrium of the invaded pest is again approximately 1.5 orders of magnitude lower than the environment's carrying capacity.
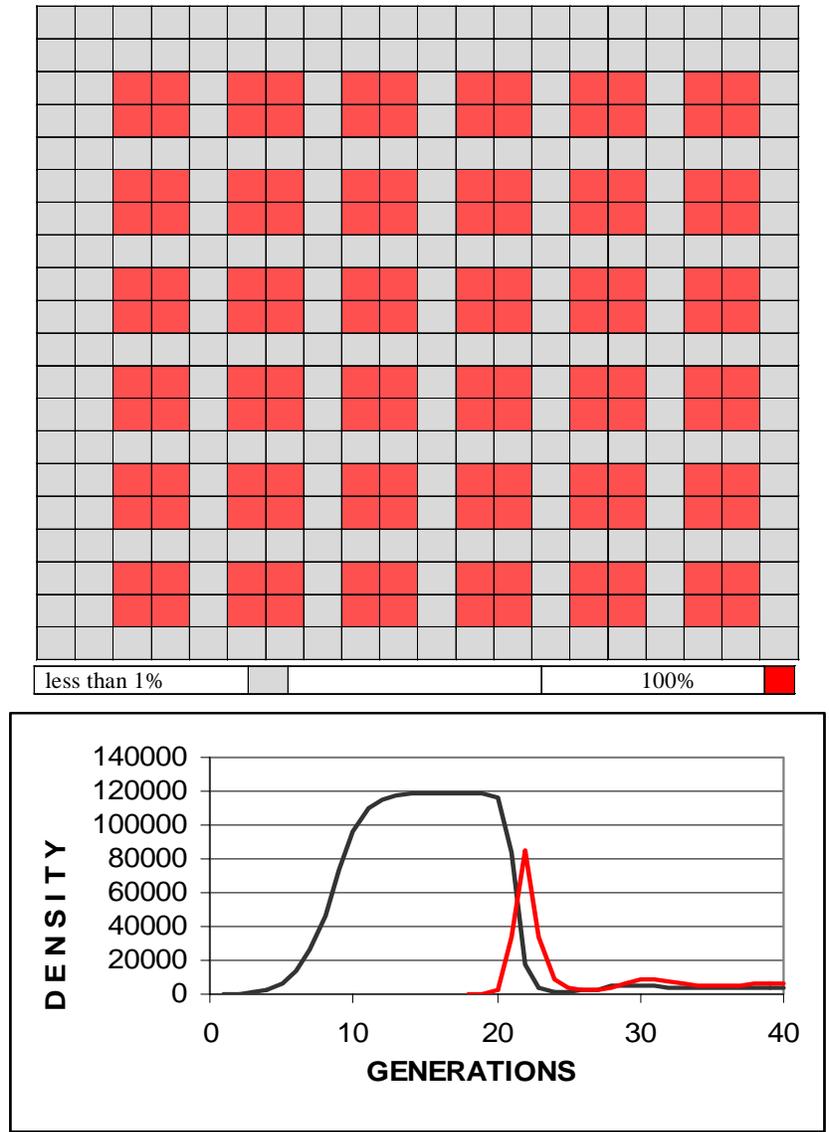
Figure 5. An environment with regularly distributed suitability for pest survival, separated by regions where the pest cannot survive. The density of the pest (black) increased until the introduction of the natural enemy (red).
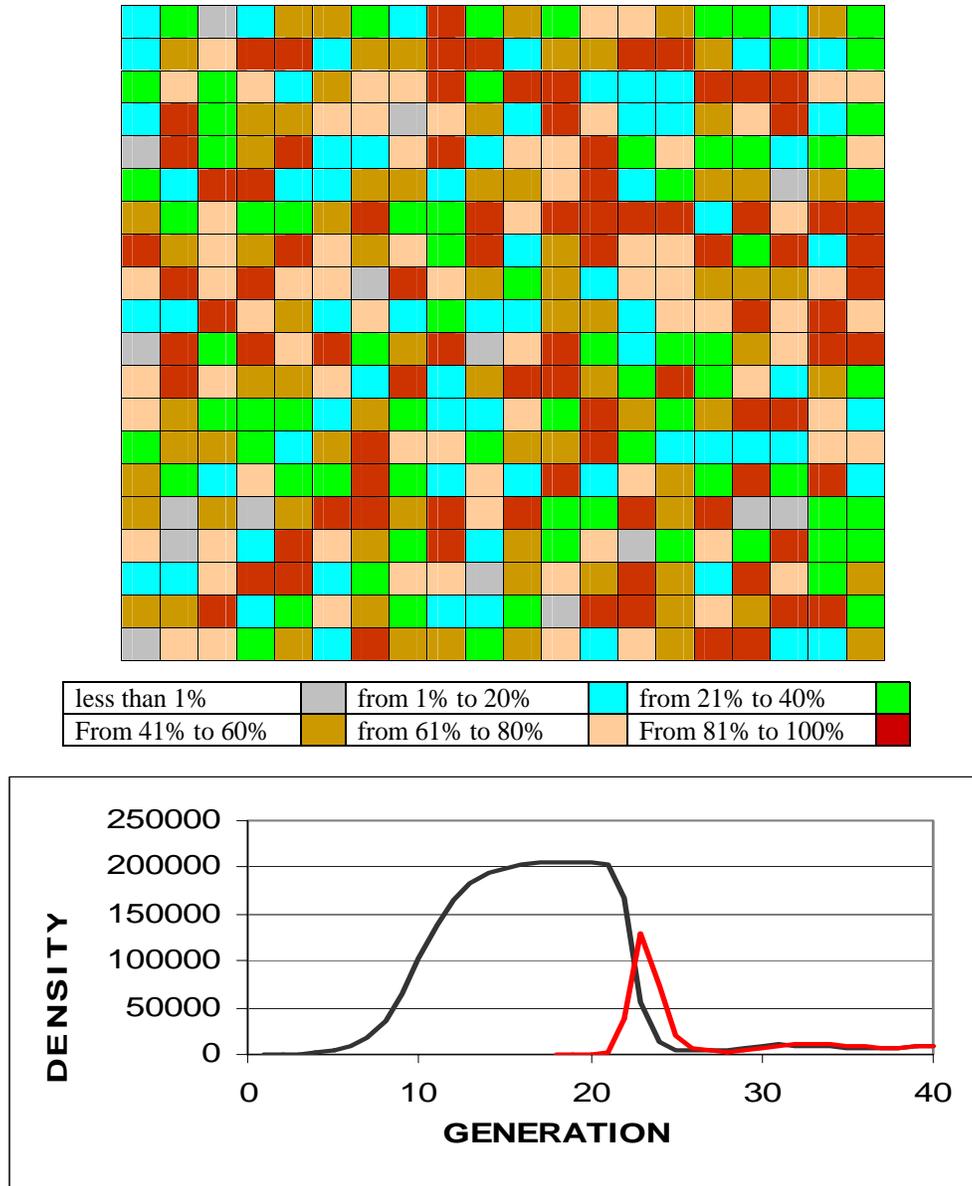
less than 1%		from 1% to 20%		from 21% to 40%	
From 41% to 60%		from 61% to 80%		From 81% to 100%	

Figure 6. An environment with randomly distributed suitability for survival of an invaded species, and the dynamics of the pest (black) increasing in number until the introduction of the natural enemy (red).

11

DISCUSSION

When discussing models and their uses, particularly I think in the field of population dynamics, one can be tempted to wax poetic on the charming attributes of this equation or that formulation, or on the elegance of a particular mathematical framework. But jesting aside, models rally only serve two sensible purposes. First, models are of great value when they shed light on some piece of truth that was previously hidden from us. How we can tell whether what the model tells us is true, since we had not discovered it ourselves, is a bit of a philosophical conundrum. But we must pass on and leave the philosophers such puzzles.

Models are also useful to us when we have confidence that they actually capture the essence of an interaction, such as in a host-parasitoid interaction. We can gain such confidence by comparing certain features of a model with similar features of a living system. If the two systems, one living on its own, and the other living in our heads, provide similar answers to questions put to both, then our confidence in the model's ability grows. It becomes a tool that we can apply to other systems. We can use it to ask questions about bigger, or broader, systems. That is what we did here.

The model that I worked with gave confidence in the beginning because it could readily mimic the behavior of simple real-world systems. This prompts the questions: Can it tell us something we do not know about more complex systems? So I applied it to imaginary ecosystems, with imaginary properties (such as migration), and gathered some new information. The model showed that biological control may well be a phenomenal tool to solving invaded species problems. It indicated that several different kinds of ecosystems that biological control could reduce the density of an invading species from 10-100-fold (although we see values far higher than that in studies of natural systems). The model also indicated that the new lower population density would be extremely stable, and would remain so for a long time. Both of these points are reasons for biological control to stand ready to aid whenever an invasive species problems crops up – not only in our traditional agricultural arenas, but also in urban areas, in forests, in the invasions of wetlands.

The question of whether or not biological control can contribute to restoring ecosystems disturbed by species invasions still needs to be answered in the field. But everything I have found, using tools as disparate as simple populations models to holistic systems analysis, tells me that the answer may well be a resounding yes.

REFERENCES

Bellows, T. S. Jr. 1981. The descriptive properties of some models for density dependence. *Journal of Animal Ecology* **50**, 139-156.

Huffaker, C. B., Messenger, P. S., and DeBach, P. 1971. The Natural Enemy Component in Natural Control in the Theory of Biological Control. *In* "Biological Control" (C. B. Huffaker, Ed.), pp. 16-67. Plenum Press, New York.

Ives, W. G. H. 1976. The dynamics of larch sawfly (Hymenoptera: Tenthredinidae) populations in southeastern Manitoba. *Canadian Entomologist* **108**, 701-730.

May, R. M., and Hassell, M. P. 1988. Population dynamics and biological control. *Philosophical Transactions of the Royal Society of London, Series B* **318**, 129-169.

Maynard Smith, J. and Slatkin, M. 1973. The stability of predator-prey systems. *Ecology* **54**, 384-391.

Nicholson, A. J. 1933. The balance of animal populations. *Journal of Animal Ecology* **2**, 131-178.

Thompson, W. R. 1924. La théorie mathematique de l'action des parasites entomophages et le facteur du hazard. *Annales de la Faculté Science de Marseille* **2**, 69-89.

Van Driesche, R. G. and Bellows, T. S. Jr. 1996. "Biological Control," Chapman and Hall, New York.

13

CLASSICAL BIOLOGICAL CONTROL OF THE ALFALFA WEEVIL IN JAPAN

Masami TAKAGI[1], Masami OKUMURA[2], Megumi SHOUBU[2], Akinori SHIRAISHI[2], and Takatoshi UENO[3]

[1]Institute of Biological Control, Faculty of Agriculture, Kyushu University
Fukuoka 812-8581, Japan
mtakagi@grt.kyushu-u.ac.jp.

[2]Moji Plant Protection Station, Ministry of Agriculture Forestry and Fisheries of Japan
Fukuoka 801-0841, Japan

[3]Institute of Biological Control, Faculty of Agriculture, Kyushu University
Fukuoka 812-8581, Japan

ABSTRACT

The alfalfa weevil was accidentally introduced into Japan in early 1980's and has been heavily infesting the Chinese milk vetch in paddy fields ever since. Chinese milk vetch is main source of honey products for apiarists in spring. Thus, the alfalfa weevil is not a pasture pest but a pest of apiculture. Four species of parasitoids were introduced into Japan as biological control agents for this pest from U.S.A. in 1988 and 1989. One of the parasitoids, *Bathyplectes anurus* was recovered in 1997. The percentage parasitism by *B. anurus* is higher on Narrow-leafed vetch in surrounding grasslands than on the Chinese milk vetch in paddy fields, suggesting that the conservation of these grasslands is important for the biological control of the alfalfa weevil.

INTRODUCTION

The alfalfa weevil, *Hypera postica* (Gyllenhal) (Coleoptera: Curculionidae) is the most serious pest of alfalfa in the United States (USDA 1991). This pest is of Eurasian origin and was accidentally introduced into North America. Classical biological control of this pasture pest has a had almost 100 years of history in the U.S.A. and this has been summarized by Radcaliffe *et al*. (1998). In all, 12 species of natural enemies were involved in the combined USDA biological control program against the alfalfa weevil (Bryan *et al*. 1993). In most major American alfalfa production areas, several natural enemies of the alfalfa weevil are now well established and alfalfa growers benefit from their effects (Radcaliffe *et al*. 1998).

The alfalfa weevil was also accidentally introduced into Japan during the early 1980's (Okumura 2002), however, its impact on alfalfa has thus far been limited because it has yet to reach the commercial alfalfa production areas located near Hokkaido. The crop heavily in-

fested by the weevil is Chinese milk vetch (*Astragalus sinicus* L.), grown in paddy fields during the early spring. Japanese rice farmers keep Chinese milk vetch as green manure in winter and the flowers of the plant provide the main source of honey products for apiarists during spring. Thus, the alfalfa weevil is not a pasture pest but more a pest of the paddy field agro-ecosystem during the non-crop season in Japan.

Moji Plant Protection Station introduced four species of parasitoids from U.S.A. into Japan for the biological control of this pest, (Kimura and Kaku 1991). One of the parasitoids, *Bathyplectes anurus* (Thomson) (Hymenoptera: Ichneumonidae) was recently recovered and is expanding its distribution. In this paper, we summarize the invasion biology of the alfalfa weevil in Japan and efforts towards its classical biological control. We also discuss the importance of natural enemy conservation and the future prospects of biological control of the alfalfa weevil.

INVASION BIOLOGY OF THE ALFALFA WEEVIL IN JAPAN

The alfalfa weevil was first discovered near Fukuoka airport in 1982 (Kimura *et al.* 1988). Subsequent surveys in the same year revealed that it was present in an area close to Fukuoka airport and widely distributed in Okinawa Island (Fig. 1). After that, the alfalfa weevil expanded its distribution towards eastern and northern Japan and has now reached Tokyo. The alfalfa weevil infests leguminous plants such as *Astragalus sinicus* (Chinese milk vetch), *Medicago lupulina* (black medick), *M.hispida* (burr medic), *M. sativa* (alfalfa), *Melitotus officinalis* (yellow sweet clover), *Trifolium pratense* (red clover), *T. repens* (white clover), and *Vicia sativa* (narrow-leaved vetch) in Japan (Yoshida *et al.* 1987). All of these leguminous plants in Japan are wild except alfalfa in Hokkaido, a northern island of Japan, and Chinese milk vetch in paddy fields of south and western Japan.

The larvae of the alfalfa weevil infest and seriously damage Chinese milk vetch flower buds and flowers in early spring. The production of honey from this source is greatly decreased as a consequence. When the farmers begin to flood the fields in May, the new adult weevils are forced to emigrate from paddy fields to aestivate following their emergence. These flooding events also displace natural enemies. After harvesting rice in the autumn, farmers seed with Chinese milk vetch to fertilize the fallow paddy fields and adult weevils are able to return to the fields. Adult female weevils oviposit on alfalfa during the winter and early spring, and larvae hatch and start damaging alfalfa from February to May.

INTRODUCTION EFFORTS OF NATURAL ENEMIES

Some indigenous parasitoids attack the alfalfa weevil but the percentage parasitism is very low and ineffective in suppressing populations of the alfalfa weevil (Okumura 1987). In order to conserve the paddy field agro-ecosystem during winter and spring, four species of parasitoids, *Bathyplectes anurus*, *B. curculionis* (Thomson), *Microctonus aethiopoides* Loan (Hymenoptera: Braconidae) and *M. colesi* Drea, were introduced as biological control agents of the alfalfa weevil from U.S.A. into Japan during 1988 and 1989 (Kimura and Kaku 1991).
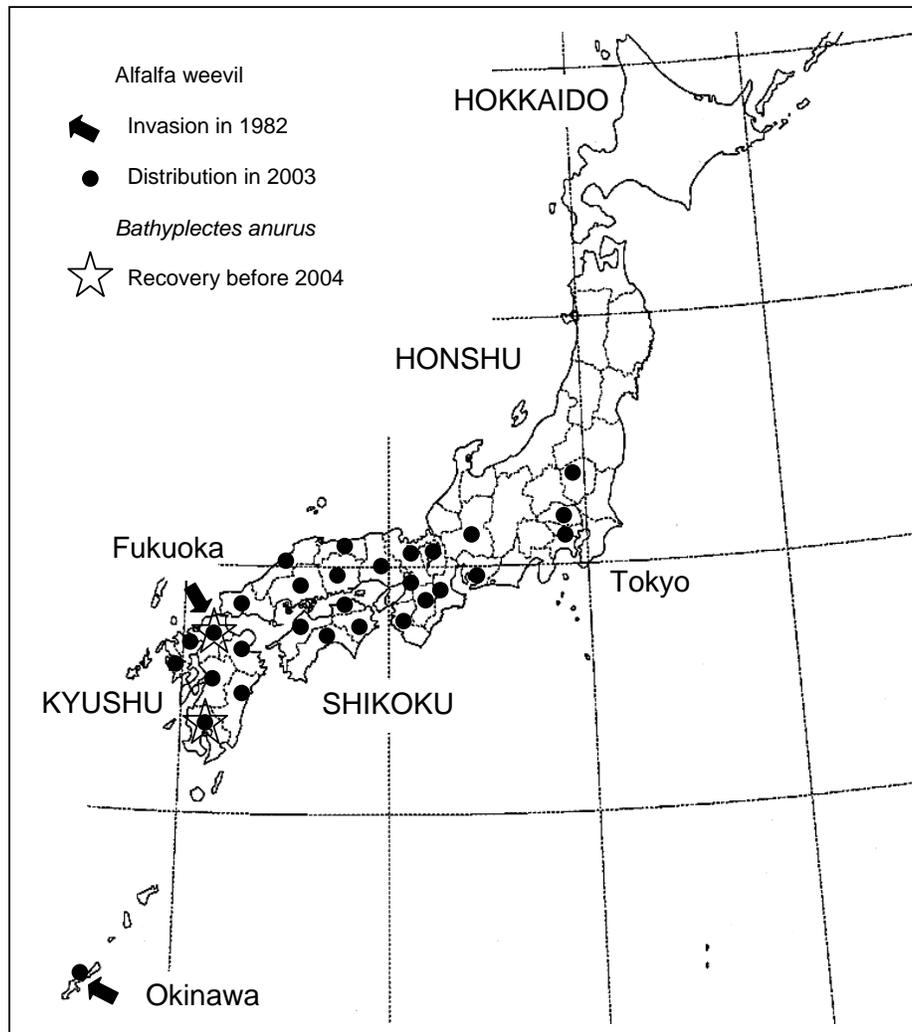
15

Figure 1. Invasion and geographic spread of the alfalfa weevil, *Hypera postica,* and recovery of its parasitoid, *Bathyplectes anurus* in Japan.

These parasitoids, except for *M. colesi,* were repeatedly released mainly in Kyushu after mass production in the laboratory. Despite these efforts, no parasitoids were considered established until 1996 (Okumura *et al.* 2002). One of the reasons for failure is that rice fields are tilled and irrigated before they are planted in the growing season. Because of these agricultural practices, both the alfalfa weevil and natural enemies disappear from the paddy fields in summer and this limits establishment. One parasitoid, *B. anurus,* however, was recovered in Fukuoka during 1997. Initially during establishment, the percentage parasitism was low but it increased gradually, reaching about 40% by 2003 (Shoubu *et al.* unpubl.). *B. anurus* is a univoltine, solitary, endoparasitoid of the alfalfa weevil larvae and its life cycle is well synchronized with its host in Kyushu (Okumura *et al.* 2002). Our survey showed that weevil damage on Chinese milk vetch was reduced from 2001 to 2003. Another survey reported higher parasitism by *B. anurus* on weevils in wild leguminoseae (e.g., *M. hispida and V. sativa*) in surrounding grasslands than on weevils in Chinese milk vetch from paddy fields (Okumura 2002).
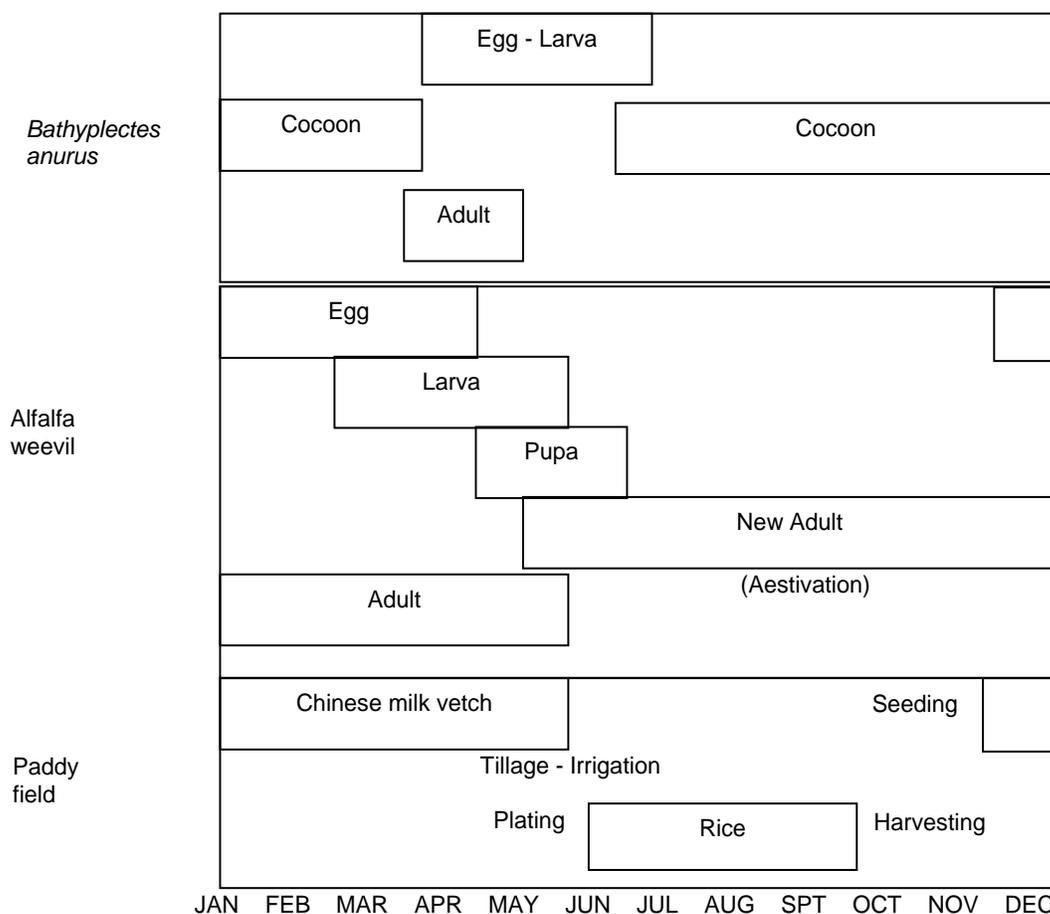
Figure 2. Life cycle of the alfalfa weevil, _Hypera postica_ and its parasitoid, _Bathyplectes anurus_ in a Japanese paddy field system.

17

DISCUSSION

Biological control of the alfalfa weevil has been of great economic benefit to U.S.A. alfalfa producers (Radcliffe _et al_. 1998). Shoubu _et al_. (2004) suggested that _B. anurus_ was a promising agent for classical biological control of alfalfa weevil in Japan, Thus, a redistribution program for _B. anurus_ is highly recommended for management of the alfalfa weevil in Japan. However, Japanese paddy agro-ecosystems are not very favourable for classical biological control because they are completely disrupted once a year during the late spring. Populations of _B. anurus_ seem to be better maintained on wild leguminous plants in surrounding grasslands than on Chinese milk vetch in paddy fields. This suggests that conservation of grasslands surrounding paddy fields is very important if the effectiveness of _B. anurus_ as a control agent for the alfalfa weevil is to be increased.

ACKNOWLEDGEMENTS

REFERENCES

Bryan, M. D., Dysart, R. J., and Burger, T. L. 1993. Releases of introduced parasites of the alfalfa weevil in the United States, 1957-1988. *US Dep. Agric. Anim. Plant Health Insp. Ser., Misc. Publ.* No. 1504, 203 pp.

Kimura, H., Okumura, M., and Yoshida, T. 1988. The occurence of the alfalfa weevil and its recent damage in Japan. *Shokubutu Boeki* (*Plant Protection*) **42**, 498-501 (in Japanese).

Kimura, H., and Kaku, K. 1991. Rearing and release of imported parasitoids of the alfalfa weevil, *Hypera postica*. *Shokubutu Boeki* (*Plant Protection*) **45**, 50-54 (in Japanese).

Okumura, M., Okamoto, T., and Yoshida, T. 1987. Natural enemies of the alfalfa weevil, *Hypera postica* (GYLL.) (Coleoptera: Curculionidae), in Japan (I). *Res. Bull. Pl. Prot. Japan* **23**, 63-65 (in Japanese with English summary).

Okumura, M. and Shiraishi, A. 2002. Establishment of the alfalfa weevil parasitoid and its potential for biological control. *Shokubutu Boeki* (*Plant Protection*) **56**, 329-333 (in Japanese).

Radcliffe, E. B., and Flanders, K. L. 1998. Biological control of the alfalfa weevil in North America. *Integrated Pest management Reviews* **3**, 225-242.

USDA 1991. Biological control of the alfalfa weevil. USDA/APIS Program Aid 1321.

Yoshida, T., Okumura, M., Sadoshima, T., Takagi, S., Okamoto, T., and Baba, K. 1987 Studies on the ecology of the alfalfa weevil, *Hypera postica* (Gyll)(Coleoptera: Curculionidae) 3. Records of observations on host plants. *Res. Bull. Pl. Prot. Japan* **23**, 33-37 (in Japanese with English summary).

18

THE INVASION OF THE WESTERN CORN ROOTWORM, *DIABROTICA VERGIFERA VIRGIFERA*, IN EUROPE AND POTENTIAL FOR CLASSICAL BIOLOGICAL CONTROL

Stefan TOEPFER[1], Feng ZHANG[1], Jozsef KISS[2], and Ulrich KUHLMANN[1]

[1] CABI Bioscience Switzerland Centre, Rue des Grillons 1
2800 Delémont, Switzerland
stoepfer@gmx.net, f.zhang@cabi.org, u.kuhlmann@cabi.org

[2] St. Istvan University, Plant Protection Department,
Pater K. u. street 1,
2100 Gödöllö, Hungary
Jozsef.Kiss@mkk.szie.hu

ABSTRACT

The maize-destroying western corn rootworm, *Diabrotica virgifera virgifera* LeConte (Coleoptera: Chrysomelidae) originates from Mexico and is an invasive species in the United States and in Europe. *Diabrotica v. virgifera* was accidentally introduced into Europe near Belgrade in Serbia in 1992. Within 10 years, this invasive alien species spread throughout Central Europe. Recently, several new spots of isolated invasions were reported in Europe showing that *D. v. virgifera* is a very successful invader. Its major success is suggested to result from: (a) suitable pathways for multiple introduction events; (b) the high flight ability of the beetle, which allows a successful initial colonization movement towards maize fields; (c) a high rate of success in pheromone-mediated mate location even at small initial population sizes; and (d) a high potential fecundity. Furthermore, this success of invasion does not seem to be reduced by the high generational mortality of more than 99% or the low realized fecundity, both of which should reduce the probability of establishment and population growth. Conclusively, European maize production is threatened. Classical biological control could be one element of a sustainable management strategy against *D. v. virgifera.* After conducting reviews, surveys and experiments on potential classical biological control agents, the following conclusions were compiled from a detailed step-by step approach: (1) effective indigenous natural enemies are not attacking any life stage of *D. v. virgifera* in Central Europe; (2) in the area of origin surveyed, *Celatoria compressa* Wulp (Diptera: Tachinidae) was the only parasitoid found on the target species, *D. v. virgifera*, and its host range is considered to be restricted to Diabroticite beetles; (3) prior to its potential importation, the parasitoid's basic and reproductive biology has been clarified; and (4) according to the results of host specificity testing, *C. compressa* would be safe for introduction as direct and indirect impacts on other organisms would be extremely low. Therefore a sustainable integrated management approach is likely to incorporate classical biological control with other control measures such as tolerant maize varieties and crop rotation.

19

INTRODUCTION

The western corn rootworm, *Diabrotica virgifera virgifera* LeConte (Coleoptera: Chrysomelidae) as well as its host plant *Zea mays* L. (Poaceae) evolved together in the subtropics of Mexico and Central America, and are non-native species in Europe. *Diabrotica v. virgifera* was accidentally introduced into Europe and was first observed near Belgrade in Serbia in 1992 (Kiss *et al.* 2005). Within 10 years, this invasive alien species spread over 310,000 km² throughout Central Europe and its eradication became impossible (Kiss *et al.* 2005). Recently, several new spots of isolated invasions were reported, such as in Lombardy (Italy), near Paris (France), near Basel (France and Switzerland), Amsterdam (The Netherlands), and London (UK) showing that *D. v. virgifera* is a very successful invader (Kiss *et al.* 2005), and will significantly change European maize production systems. Pathways of introductions of *D. v. virgifera* have never been formally investigated. The theory of introduction into Europe from North America via airplanes is generally accepted (Kiss *et al.* 2005). Possible causes of the successful invasiveness of *D. v. virgifera* theoretically include: (a) suitable pathways for multiple introduction events; (b) a remarkable flight ability of the beetle, which allows successful initial colonization movements towards maize fields; (c) a low viable population size required to build up a population; (d) a high capability of finding the counter sex for copulation at small initial population sizes by using sex pheromones; (e) a low mortality of developmental stages of *D. v. virgifera* in the invaded areas; and (f) a high fecundity.

Due to the successful invasion of *D. v. virgifera* in Europe, a sustainable management strategy against this invasive alien pest is needed. Classical biological control may have an important application in such a management policy as it provides an opportunity to partially reconstruct the natural enemy complex of an invading alien pest. *Diabrotica v. virgifera* is considered a prime target for a classical biological control approach. In order to investigate the initial colonization process of this invasive alien pest towards maize fields, mark-release-recapture studies were conducted in southern Hungary in 2003 and 2004. To study the potential use of classical biological control, life table studies were used to find host niches of *D. v. virgifera* that are not presently occupied by indigenous natural enemies in the area of invasion. Based on this information, specific and effective natural enemies from the area of origin were selected and investigated for potential introduction into Europe. Over the last five years we evaluated the potential of classical biological control applying a step-by-step approach: (1) investigating the initial colonization process of introduced *D. v. virgifera*; (2) conducting life table studies for *D. v. virgifera* in the area of invasion and studying the minimum viable population size of *D. v. virgifera*; (3) surveying for natural enemies in the area of invasion and origin; and (4) assessing the suitability and host specificity of candidate biological control agents.

MATERIALS AND METHODS

MARK-RELEASE-RECAPTURES DURING THE INITIAL COLONIZATION PROCESS OF INTRODUCED *D. V. VIRGIFERA*

Mark - release - recapture studies were conducted in southern Hungary in order to investigate the movements of *D. v. virgifera* towards suitable habitats, such as to its host plant maize

(for details refer to Toepfer *et al.* 2004). In 2003 and 2004, nine mark-release-recapture experiments were carried out in a grass steppe-area and alfalfa field, in which two small maize fields had been planted 300 m distant from the release points. After each release of 5,500 to 6,000 *D. v. virgifera*, adult beetles were recorded three times every second day by non-baited yellow sticky traps placed at regular intervals around the release point. The probability of arrival of female beetles in maize field was estimated to assess the risk of establishment of starter populations.

LIFE-TABLE STUDY TO MEASURE MORTALITY FACTORS AND MINIMUM VIABLE POPULATION SIZE

Life-table studies of this univoltine species were conducted in two maize fields in southern Hungary from 2000 to 2003 in order to provide an ecological understanding of mortality factors regulating population dynamics of this invasive pest (for details refer to Toepfer and Kuhlmann 2005). The mortality affecting the egg stage was assessed by exposing several thousand eggs to pre-overwintering, overwintering and post-overwintering conditions and by recovering the surviving eggs. The mortality levels of larval to adult stages were measured by artificially infesting 286 maize plants and subsequently recovering (1) the three larval instars and pupae at six time intervals using soil-root sampling and (2) the adults using emergence cages. Three age-specific life-tables were constructed. Finally, the reproductive rates of small founding populations were calculated to discern the minimum viable population size.

NATURAL ENEMY SURVEY IN THE AREA OF INVASION AND ORIGIN

A three-year field survey was conducted in Hungary, Yugoslavia, and Croatia, which are currently the focal points of invasion, to determine the occurrence of indigenous natural enemies of *D. virgifera* in Europe. A total of 9,900 eggs, 550 larvae, 70 pupae and 33,000 adults were examined for the occurrence of parasitoids, nematodes, and fungal pathogens. Moreover, the above-described life-table study was used to determine host niches of *D. v. virgifera* that are not presently occupied by indigenous natural enemies. In a next step, the structure and function of natural enemies in the area of origin of *D. v. virgifera* was assessed, with a special emphasis placed on parasitoids of *Diabrotica* adults. Surveys were conducted in collaboration with Dr. Astrid Eben (Instituto de Ecologia, Xalapa, Mexico) and Dr. Rebeca Alvarez Zagoya (Instituto Politecnico Nacional, CIIDR-IPN, Durango, Mexico). Adults of *Diabrotica* spp. were collected in agricultural and natural habitats containing a high species diversity including the target species *D. v. virgifera* in northern Mexico. In collaboration with G. Cabrera Walsh, (USDA-ARS South American Biological Control Laboratory, Buenos Aires, Argentina) *Diabrotica* adult natural enemy surveys were carried out in central and northern Argentina as well as southeastern Brazil. *Diabrotica* adults were collected directly from leaves and flowers of maize, beans, squash or wild plants within the fields. In all surveys, every available species of the sub-tribe Diabroticina, e.g. *Diabrotica spp., Acalymma spp*., and *Ceratoma spp*., were collected. *Diabrotica* adults were separated based on species, collection site and collection date and colonies were maintained in cages until emergence of parasitoid larvae. Based on the original host ranges of the parasitoids discovered, as well as their respective parasitism rates and overwintering strategies, the most promising parasitoid species was selected for further studies.

SUITABILITY AND HOST SPECIFICITY OF THE CANDIDATE BIOLOGICAL CONTROL AGENT

In order to study in detail the suitability of the selected candidate biological control agent, Celatoria compressa Wulp (Diptera: Tachinidae), the following attributes were investigated: (a) behavior of host attacks by C. compressa females, (b) the larviposition period, (c) the number of daily larviposition attempts per female, (d) the number of puparia produced daily per female and (e) the cumulative puparia production per female over the entire larviposition period (for details refer to Zhang et al. 2003). The functional response of C. compressa was also studied. A randomly chosen density between one and 50 adults of D. v. virgifera was offered to an individual 8 to 10 day-old mated female for 24 hours. After exposure, the hosts were kept for 20 days and emerged C. compressa larvae were recorded for each host density.

With respect to the safety of biological control, standards and frameworks recently developed for the release of exotic biological control agents were followed (van Lenteren et al. 2003). This study focused first on the selection of potential non-target species at risk in *D. v. virgifera* invaded areas in Europe, and secondly on host specificity testing of *C. compressa*. According to the phylogenetic centrifugal method proposed for weed biological control agents and a practical approach suggested by Kuhlmann and Mason (2003), a simplifying procedure was applied and indigenous Coleopteran species were selected for testing under quarantine laboratory conditions (for details refer to Kuhlmann et al. 2005). Thereafter, the host specificity of the candidate classical biological control agent C. compressa was assessed in (1) no choice tests, (2) sequential no choice tests, (3) choice tests, and (4) sequential choice tests.

RESULTS

INITIAL COLONIZATION PROCESS OF INTRODUCED *D. V. VIRGIFERA*

In five out of 15 recapture periods, released *D. v. virgifera* populations performed a uni-directional movement (38%), in three cases beetles performed a bi-directional movement (20%), and in seven cases no directional movement was found (46%). In ten out of 15 recapture periods, the released populations were moving in a direction that was comparable with the mean wind direction. Averaging over sites and years, *Diabrotica* beetles did not move in the directions of the two small maize fields more frequently than expected if assuming random movement. However, beetles did travel significantly more frequently in the direction of naturally occurring maize fields (within a radius of 1,500 m) than towards other habitats. On average, 2.8% ± 3.2 SD of all recaptured *Diabrotica* beetles arrived in a 300 m distant small maize plot.

MORTALITY FACTORS AND MINIMUM VIABLE POPULATION SIZE

A total mortality of 99.6% ± 0.16 SD was determined during the time period between oviposition and the emergence of adults. Highest losses were generated by mortality during the first instar larval stage (94.2% marginal death rate) and by the inability of adults to realize their potential fecundity (80.4%). The most successful age intervals were pre- and post-diapausing eggs, with marginal death rates of only 17.3% and 18.4%, respectively. The third instar larvae and pupae also had a moderately low marginal death rate of 36%. Factors that

22

varied greatly between years and sites, such as realized fecundity and mortality of second and third instar larvae and overwintering eggs, had the highest potential to change population growth. *Diabrotica v. virgifera* net reproductive rates were generally below 1 (mean R_0 = 0.62) indicating declining pest populations. Therefore, the risk is low that newly introduced females of this alien beetle would produce enough eggs, larvae and emerging adults to establish a new generation. However, when considering the maximum potential progeny of females, the capacity of increase could reach growth factors between 2 and 4.5. Luckily, only 19.6% of this potential fecundity was usually realized under field conditions and the mean realized fecundity of starter populations varied substantially between years and between individual females.

NATURAL ENEMY SURVEY IN THE AREA OF INVASION AND ORIGIN

The natural enemy survey as well as the life-table study revealed that effective indigenous natural enemies were generally not attacking any of the life stages of *D. v. virgifera* in Europe. Two exceptions were the fungi *Beauveria bassiana* (Bals.) Vuill. (Mitosporic fungi; formerly Deuteromyces) and *Metarhizium anisopliae* (Metsch.) Sorok (Mitosporic fungi) attacking adults of *D. v. virgifera* on an extremely low level (< 1%). However no other entomopathogenic fungi, entomopathogenic nematodes, or parasitoids were found on eggs, larvae, pupae or adults. Therefore, each life stage of *D. v. virgifera* would be a suitable target for a classical biological control agent, and the natural enemy complex of the invading alien *D. v. virgifera* may be reconstructed in Europe.

Based on survey results and literature records in the area of origin of *Diabrotica spp.* (Cabrera Walsh *et al.* 2003; Eben and Barbercheck 1996; Guimaraes 1977; Heineck-Leonel and Salles 1997), adult parasitoids are probably the most common natural enemies of species in the *virgifera* group of the genus *Diabrotica*, followed by mermithid nematodes of the genus *Hexamermis* (Eben and Barbercheck 1996; Kuhlmann and Burgt 1998). As the focus of this survey was to obtain parasitoids of adult *Diabrotica*, knowledge of natural enemies attacking the soil dwelling larval stages of *Diabrotica* beetles is still incomplete. In the classical biological control agent selection process, five of the six known parasitoid species of adult *Diabrotica* in the area of origin were excluded from consideration based on information gleaned from the literature. The North and Central American tachinid fly, *Celatoria setosa* was not selected as Fisher (1983) indicated that this fly is almost exclusively a parasitoid of *Acalymma* species. Similarly, the North American tachinid fly, *Celatoria diabroticae* Gahan was also not chosen because it appears to be strongly associated with only *Diabrotica undecimpunctata howardi* Barber (Summers and Stafford, 1953), and *D. undecimpunctata undecimpunctata* Mannerheim (Fischer, 1981). The North American braconid *Centistes diabroticae* was not considered as it has been only reared from *Acalymma vittata* (F.) (Gahan, 1922; Fischer, 1981). Experimental data indicated that the South American *Celatoria bosqi* will not accept *D. v. virgifera* adults as hosts, which suggested that this tachinid appears to be specific to the *fucata* group within the genus *Diabrotica*. The South American braconid *Centistes gasseni* Shaw was rejected as a potential biological control agent due to the parasitoid's incompatible overwintering strategy and rearing difficulties. The only parasitoid actually found on the target species, *D. v. virgifera,* was the tachinid *Celatoria compressa* from northern Mexico. It attacked a range of species in four different genera of Diabroticite beetles suggesting a large

number of host species, but nonetheless restricted to Diabroticite beetles. *Celatoria compressa* was ultimately the only parasitoid that was selected as a candidate biological control agent for *D. v. virgifera* in Europe based on its availability in northern Mexico, its known host range including the target host record, and its suitability for rearing under laboratory conditions. Generally, it should be noted that distribution and the efficacy known for *C. compressa* should be considered as provisional due to the fact that these tachinid species have been little studied.

SUITABILITY AND HOST SPECIFICITY OF THE CANDIDATE BIOLOGICAL CONTROL AGENT

The age of *C. compressa* adults was found to be the most crucial factor in achieving mating. Only newly emerged, one hour-old females mated successfully with 2 to 5 day-old males. During the pre-larviposition period, the egg load of females increased steadily from day one (mean = 16.6 ± 1.1 SE) to a maximum egg load on day four (mean = 69.3 ± 0.8 SE). During a female's larviposition period (mean = 22.5 ± 0.6 SE days; n = 19), a total of 33.2 ± 0.9 SE first instars were larviposited into hosts. This represents only half of the female's egg load. The cumulative number of larviposition attempts per female reached a mean of 120 ± 2.2 SE, whereas the mean cumulative puparia production per female was only 29.7 ± 5 SE. The number of hosts parasitised by *C. compressa* increased with increasing host density until an upper limit was reached. This functional response of *C. compressa* fit the Holling type II response (R^2 = 0.239; F = 96.40; df = 2, 80; $P < 0.001$).

Nine European non-target Coleopteran species potentially at risk of being attacked by *C. compressa* were selected as representative species for testing in the quarantine laboratory: two-spotted lady beetle, *Adalia bipunctata* L. (Coleoptera: Coccinellidae); red pumpkin beetle, *Aulacophora foveicollis* Lucas (Coleoptera: Chrysomelidae: Galerucinae: Luperini); thistle tortoise beetle, *Cassida rubiginosa* Müller (Coleoptera: Chrysomelidae: Cassidinae); golden loosestrife beetle, *Galerucella pusilla* Duft (Coleoptera: Chrysomelidae: Galerucinae: Galerucini); green dock beetle, *Gastrophysa viridula* Deg. (Coleoptera: Chrysomelidae: Chrysomelinae); *Gonioctena fornicata* Brüggemann (Coleoptera: Chrysomelidae: Chrysomelinae); cereal leaf beetle, *Oulema melanopus* (L.) (Coleoptera: Chrysomelidae: Criocerinae); elm leaf beetle, *Pyrrhalta luteola* (Müller) (Coleoptera: Chrysomelidae: Galerucinae: Galerucini); and pea and bean weevil, *Sitona lineatus* Linnaeus (Coleoptera: Curculionidae).

In no-choice or choice tests, naïve females of C. *compressa* never parasitised eight of nine non-target species tested. In the absence of *D. v. virgifera* adults, *A. foveicollis* was occasionally accepted (6 larvae in 260 hosts), but complete development by *C. compressa* was not achieved. The acceptance of *A. foveicollis* by *C. compressa* was significantly lower than that of the target host, *D. v. virgifera,* 2.3% versus 28.7%. In the sequence of no-choice tests, *A. foveicollis* was accepted (4 larvae in 260 hosts) but it was again significantly lower than that of the target species compared within the same day of three successive days. From the four *A. foveicollis* adults parasitised, a single *C. compressa* larva completed its development and formed a puparia. In the presence of *D. v. virgifera* in the choice test, *A. foveicollis* was never accepted by *C. compressa* but during the sequence of choice tests *A. foveicollis* was again accepted by

24

C. compressa in a few cases. However, host acceptance was significantly lower than that observed for *D. v. virgifera* on the first, second and third day. In contrast to the results of the sequence of no-choice tests, host suitability for *A. foveicollis* by *C. compressa* was not found.

It can be predicted that the candidate biological control agent *C. compressa* will have a narrow host range in Europe, being restricted to a few genera on the tribe level of Luperini among the subfamily Galerucinae. These results of the physiological host range of *C. compressa* obtained under quarantine conditions are in agreement with the known field host range from the area of origin in Mexico.

DISCUSSION AND CONCLUSIONS

Accidentally introduced specimens of the invasive alien maize pest, *D. v. virgifera*, must initially migrate to their target habitat, maize, in order to feed, reproduce, establish and then to invade other areas. Mark-release-recapture experiments revealed that small introduced *Diabrotica* beetle populations mainly show non-directional dispersal. However, beetles were moving significantly more frequently towards commercial scale maize fields within a radius of up to 1,500 m than in the direction of other habitats. Adult populations of *D. v. virgifera* were spreading over more than 100 hectares of non-maize areas, and 2.8% of all recaptured beetles arrived in maize plots at a distance of 300 m from the release point. This probability of arrival would increase linearly with the number of maize fields. Next to this number of maize fields, the number of introduced specimens is essential to estimate risk of arrival of *D. v. virgifera* in their target habitat. Literature references suggest that in most cases hardly more than 10 specimens are introduced in a single event of introduction (Wittenberg and Cock 2001). However, in a hypothetical case where 10 maize fields are in close proximity to a point of alien introduction, already one to two females out of the ten *Diabrotica* beetles would reach a maize field, leading to a risk of establishment of a starter population of the introduced species. Fortunately, there would be a less than 1 % chance that those newly arriving female beetles would produce enough progeny to ensure the successful emergence of a new adult generation. The rate of increase from a starter population to the following generation was often found to be less than factor one, which indicates declining populations and would result in the extinction of introduced founder populations. However, when considering the maximum potential progeny of females, the capacity of increase could reach growth factors between 2 and 4.5. Luckily, only 19.6 % of this potential fecundity was usually realized under field conditions and the mean realized fecundity of starter populations varied considerably between years and between individual females. Due to this variability it remains difficult to predict the probability and quarantine risk for establishment of newly introduced starter populations. Still, the high percentage of non-directional flight by adults, the moderate probability of accidentally introduced specimens to arrive in maize, the low realized fecundity of females as well as the extremely low survival probability until the subsequent generation very much decrease the probability of a successful invasion of this alien *D. v. virgifera*. Reasons for the ongoing invasions in Europe must be explained by either optimal oviposition conditions or by an increased frequency of introduction events.

25

With regard to the use of classical biological control as a sustainable management strategy against *D. v. virgifera* the following conclusions are compiled:

1. Effective indigenous natural enemies are not attacking any life stage of *D. v. virgifera* in Central Europe;

2. In the area of origin surveyed, *Celatoria compressa* was the only parasitoid found on the target species;

3. Prior to its potential importation, the parasitoid's basic and reproductive biology was clarified;

4. According to host specificity testing, *Celatoria compressa* would be safe for introduction as direct and indirect impacts on other organisms would be extremely low (host range is considered to be restricted to Diabroticite beetles).

Regarding the tachinid *C. compressa*, we have studied a promising candidate classical biological control agent that would be safe for introduction against *D. v. virgifera* in Europe. Nonetheless, there are a number of questions that remain to be answered before its potential importation, such as the hibernation strategy of *C. compressa*, its cold tolerance and its impact under more natural conditions than in bioassays in quarantine laboratories. In conclusion, a sustainable integrated approach against *D. v. virgifera* in Europe is likely to incorporate classical biological control with other pest management options, such as tolerant maize varieties, crop rotation, and cultural techniques which have the potential to enhance the conservation of natural control.

26

ACKNOWLEDGEMENTS

REFERENCES

Baufeld, P., and Enzian, S.. 2005. Maize Growing, Maize High-Risk Areas and Potential Yield Losses Due to Western Corn Rootworm (*D. virgifera virgifera* LeConte) Damage in Selected European Countries. *In* "Western Corn Rootworm: Ecology and Management" (S. Vidal, U. Kuhlmann, and C. R. Edwards, Eds.), pp. 285-302. CABI Publishing, Wallingford, U.K.

Cabrera Walsh, G., Athanas, M. M., Salles, L. A. B., and Schroder, R. F. W. 2003. Distribution, host range, and climatic constraints on *Centistes gasseni* (Hymenoptera: Braconidae), a South American parasitoid of cucumber beetles, *Diabrotica spp.* (Coleoptera: Chrysomelidae). *Bulletin of Entomological Research* **93**, 561-567.

Eben, A., and Barbercheck, M. E.. 1996. Field observations on host plant associations enemies of diabroticite beetles (Chrysomelidae: Luperini) in Veracruz, Mexico. *Acta Zoologica Mexicana* **76**, 47-65.

Fisher, D. C. 1983. "*Celatoria diabroticae* Shimer and *Celatoria setosa* Coquillett:

Tachinid parasitoids of the Diabroticite Coleoptera", University of Illinois at Urbana-Champaign. University of Illinois at Urbana-Champaign, Illinois.

Guimaraes, J. H. 1977. Host-parasite and parasite-host catalogue of South America Tachinidae (Diptera). *Arquivos de Zoologia* **28**, 1 -131.

Heineck-Leonel, M. A., and Salles, L. A. B. 1997. Incidence of parasitoids and pathogens in adults of *Diabrotica speciosa* (Germ.) (Coleoptera: Chrysomelidae) in Pelotas, RS. *Anais da Sociedade Entomológica do Brasil* **26**, 81-85.

Kiss, J., Edwards, C. R., Berger, H. K., Cate, P., Cean, M., Cheek, S., Derron, J., Festic, H., Furlan, L., Igrc-Barcic, J., Ivanova, I., Lammers, W., Omelyuta, V., Princzinger, G., Reynaud, P., Sivcev, I., Sivicek, P., Urek, G., and Vahala, O. 2005. Monitoring of Western Corn Rootworm (*Diabrotica virgifera virgifera* LeConte) in Europe 1992-2003, *In* "Western Corn Rootworm: Ecology and Management" (S. Vidal, U. Kuhlmann and C. R. Edwards, Eds.), CABI Publishing, Wallingford, U.K.

Kuhlmann, U., and Burgt, W. A. C. M. 1998. Possibilities for biological control of the western corn rootworm, *Diabrotica virgifera virgifera* LeConte, in Central Europe. *Biocontrol News and Information* **19**, 59 - 68.

Kuhlmann, U., Toepfer, S., and Zhang, F. 2005. Is Classical Biological Control Against Western Corn Rootworm in Europe a Potential Sustainable Management Strategy? *In* "Western Corn Rootworm: Ecology and Management" (S. Vidal, U. Kuhlmann and C. R. Edwards, Eds.), pp. 263-284., CABI Publishing, Wallingford, U.K.

Kuhlmann, U., and Mason, P. G. 2003. Use of field host range surveys for selecting candidate non-target species for physiological host specificity testing of entomophagous biological control agents. Proceedings of the International Symposium on Biological Control of Arthropods, Honolulu, Hawaii. United States Department of Agriculture, Forest Service, Morgantown, WV, 370 –377.

Summers, T. E., and Stafford, E. W. 1953. *Diabrotica undecimpunctata howardi* parasitized by *Celatoria diabroticae. Journal of Economic Entomology* **46**,180.

Toepfer, S., and Kuhlmann, U.. 2004. Survey for natural enemies of the invasive alien chrysomelid, *Diabrotica virgifera virgifera*, in Central Europe. *BioControl* **49**, 385-395.

Toepfer, S., Szucs, M. Levay, N., and Kiss, J. 2004. Initial spread by introduced *Diabrotica virgifera virgifera* towards maize fields, 10th *Diabrotica* Subgroup Meeting of IOBC/IWGO. Engelberg, Switzerland. 41

Toepfer, S., and Kuhlmann, U. 2005. Natural Mortality Factors Acting on Western Corn Rootworm Populations: A Comparison Between the United States and Central Europe. *In* "Western Corn Rootworm: Ecology and Management" (S. Vidal, U. Kuhlmann, and C. R. Edwards, Eds.), pp. 95-119. CABI Publishing, Wallingford, U.K.

Van Lenteren, J. C., Babendreier, D., Bigler, F., Burgio, G., Hokkanen, H. M. T., Kuske, S., Loomans, A. J. M., Menzler-Hokkanen, I., Van Rijn, P. C. J., Thomas, M. B., Tommasini, M. G., and Zeng, Q. Q. 2003. Environmental risk assessment of exotic natural enemies used in inundative biological control. *Biocontrol* **48**, 3-28.

Wittenberg, R., and Cock, M. J. W. 2001. "Invasive Alien Species: A Toolkit of Best Prevention and Management Practices". CABI Publishing, Wallingford U.K.

Zhang, F., Toepfer, S., Riley, K., and Kuhlmann, U. 2003. Reproductive biology of *Celatoria compressa* (Diptera: Tachinidae), a parasitoid of *Diabrotica virgifera virgifera* (Coleoptera: Chrysomelidae). *Biocontrol Science and Technology* **14**, 5-16.

28

IDENTIFYING THE DONOR REGION WITHIN THE HOME RANGE OF AN INVASIVE SPECIES: IMPLICATIONS FOR CLASSICAL BIOLOGICAL CONTROL OF ARTHROPOD PESTS

Mark S. HODDLE

Department of Entomology, University of California
Riverside, CA 92521, U.S.A.

mark.hoddle@ucr.edu

ABSTRACT

Foreign exploration is a major component of a classical biological control program. Exploration within the home range of the target can be a daunting proposition as the target is most likely rare with an irregular distribution. As costs and greater regulatory oversight increase, classical biological control programs targeting arthropods need to complete preliminary steps prior to embarking on a collecting trip that will return live natural enemies to quarantine for rearing and evaluation. These preliminary steps should be designed to maximize the likelihood of identifying the donor region within the pest's home range from which the invading population originated. Two techniques can be used to help identify the target's donor region(s): climate matching and haplotype identification. These techniques increase the likelihood of collecting natural enemies well suited to the climate of the receiving area and will result in natural enemies best adapted to the genetic structure of the invasive target population. Further, haplotyping studies may help clarify taxonomic uncertainty regarding the "true" identity of the target pest and may also help uncover conduits by which these unwanted organisms are moving from area to area. This paper details work completed on determining the home range of the avocado thrips, *Scirtothrips perseae*, and delineating the donor region within the prescribed home range. The implications of this approach for increasing the success rates of classical biological control of arthropods are discussed.

29

INTRODUCTION

Globally, exotic species pose a perennial invasion threat, and successful invaders can be extremely damaging to agricultural, urban, and natural areas should they establish outside of their home range. Exotic pioneers are infiltrating previously unexploited ecosystems at unprecedented rates as the human population grows, as goods are transported ever more rapidly over an increasingly larger global scale, and then passed through border inspection stations with cursory examination before release tens of thousands of kilometers from the point of origin. Economic losses and associated management costs for exotic arthropod pests in the U.S.A. have been estimated to cost in excess of $20 billion annually (Pimentel *et al*. 2002), and over $2 billion for New Zealand (Barlow and Goldson 2002).

Clearly, invasive arthropod pests have not only major economic impacts but they can cause devastating effects on ecosystem functioning once they become an established unit within the accommodating system. Classical biological control, that is, the deliberate importation and release of exotic natural enemies for control of an exotic pest in a newly invaded range, can be an extremely powerful tool for suppressing pests in agricultural, urban, and natural environments (Hoddle and Syrett 2002). Many problematic arthropods of exotic origin may be good potential targets for classical biological control. In some instances, exotic natural enemies may be the only rational control option once eradication, containment, and long-term chemical suppression are deemed ineffective or unsustainable by regulatory agencies (Hoddle 2004a). Despite over 100 yrs research and application of classical biological control by arthropods against arthropods, the success rate per decade has been consistent at around 10-12% (Gurr *et al.* 2000). The success rate for classical biological control of arthropods is substantially lower than that observed for terrestrial weeds where control has been estimated at around 30% (Syrett *et al.* 2000).

Classical biological control has come under increasing scrutiny by ecologists and conservationists because natural enemies used for exotic pest suppression may pose serious and irreversible threats to non-target organisms in ecosystems in which they are released or infiltrate post-release (Louda and Stiling 2004). Despite the widely recognized economic, environmental, and social benefits that accrue from successful biological control programs it is recognized that more needs to be done to ensure greater efficacy and safety to mitigate adverse non-target effects (Hoddle 2004b). Concerns over the specificity of natural enemies used in classical biological control programs against arthropods is leading to the development and implementation of legislative guidelines that are designed to promote assessment of the safety of potential candidate biological control agents prior to release (see papers in session 13). This had the effect of promoting greater research activity on techniques that can be used to predict (see papers in session 13) and assess environmental risk (see papers in session 12) arising from the introduction of novel upper trophic level organisms into areas that have historically lacked such organisms.

In an environment of increasing regulation and given the well justified need to address concerns over natural enemy safety, it is likely that project costs will significantly increase and the numbers and types of classical biological control projects that are launched may decrease and be removed from the research agenda of public Universities to become a government enterprise (Van Driesche and Hoddle 1997). Consequently, it is becoming increasingly necessary to take as many preliminary steps as possible to gather pertinent data to maximize the likelihood of finding suitable biological control agents when initiating a classical biological control project prior to launching an expensive and time consuming foreign exploration program that will locate natural enemies that must be later subjected to safety testing. Preliminary steps must aim to increase the chances of locating host specific natural enemies in the pest's home range that are likely to have maximal impact on target population growth after being imported, cleared through quarantine, and established in the invaded range. One preliminary approach that may increase the likelihood of locating the most efficacious natural enemies is to search within specific areas of the pest's home range for agents that are most closely associated with pest populations that have the most similar biological, ecological, and genetic profile as the invading population that needs to be controlled. This article focuses on

using a climatic modeling and haplotyping approach to locating natural enemies for the biological control of avocado thrips, *Scirtothrips perseae* Nakahara (Thysanoptera: Thripidae).

DESIGNING A FOREIGN EXPLORATION PROGRAM
FOR AVOCADO THRIPS

BIOLOGY AND IMPACT OF THE INVADER

Avocado thrips (Fig. 1) was first discovered on avocados in June 1996 near Port Hueneme (Ventura County) and in Irvine (Orange County) California U.S.A. This pest currently infests 95% of California's avocado acreage and approximately 80% of commercial orchards require pesticide applications to control this pest (Hoddle *et al.* 2002). Economic losses are incurred when avocado fruit is scarred (Fig. 2) by feeding thrips adults and larvae and this pest has been estimated to cost the California avocado growers $4-5 million each year now reliable management practices have been implemented (Hoddle *et al.* 2003). At time of discovery in California, avocado thrips was a species new to science (Nakahara 1997), and nothing was known about its area of origin, biology, or ecology (Hoddle *et al.* 2002). This thrips is unusual in the genus *Scirtothrips*. It is the only species known to outbreak and cause economic damage in cool weather, all other pest species of *Scirtothrips* outbreak and cause damage when temperatures are high. Cool weather in late winter and spring in California synchronizes pest population growth with leaf flush and immature fruit growth which are initiated during spring each year (Hoddle 2002a). These two substrates are most favored by *S. perseae* for feeding and oviposition (Hoddle 2002b).

31

In California, extensive host plant surveys indicate that *S. perseae* may be monophagous as it has only been recorded breeding on avocados (Hoddle *et al*. 2002c). When taken together, pest ecology and host plant preferences, strongly suggest that *S. perseae* has a close evolutionary history with avocados and may have originated somewhere in the home range of this plant. Three distinguishable ecological races or subspecies of avocado (*Persea americana*) are recognized; these being (1) Mexican (*P. americana* var. *drymifolia*), (2) Guatemalan (*P. americana* var. *guatemalensis*) and (3) West Indian or Caribbean (*P. americana* var. *americana*)

Figure 1. Avocado thrips, *Scirtothrips perseae* Nakahara (Thysanoptera: Thripidae). Photo: UC Regents. UGA1390031

Figure 2. Avocado fruit showing scarring that has resulted from avocado thrips feeding damage when these fruit were < 2 cm in length. Photo M. S. Hoddle. UGA1390032

types. The areas of origin for these avocado races indicated where foreign exploration for avocado thrips should commence (Hoddle *et al.*, 2002c).

FOREIGN EXPLORATION STEP I: DELINEATING THE HOME RANGE OF THE PEST

Over the period 1997-2000 avocados (wild and cultivated) in Mexico, Central America, Brazil, and the Caribbean were intensively searched for avocado thrips and associated natural enemies. Collecting was repeated in Mexico and Central America in 2003 and 2004. Collection records enabled the preparation of a distribution map for *S. perseae* in Mexico and Central America (Fig. 3).

Scirtothrips perseae has a highly restricted range (Fig. 3) and is only found at elevations exceeding 1500 m. This high altitude range explains the predilection of this pest for cool growing conditions and suggests that it was pre-adapted to cool growing conditions in coastal avocado orchards in California (Hoddle *et al*. 2002c). Survey work in California indicates that this pest is most severe within 20 kms of the coast because of cooler conditions resulting from the marine influence, and hotter conditions typical of more interior and arid areas do not experience problems with this insect (Hoddle 2003).

FOREIGN EXPLORATION STEP II: DELINEATING THE DONOR REGION WITHIN THE HOME RANGE

Avocado thrips occupies a vast range within Mexico that extends into the mountainous areas of central Guatemala. Somewhere within this range it is likely that an invading population of *S. perseae* originated and entered California. More precisely defining this donor region within the home range may provide natural enemies that are closely adapted to the ecological and climatic requirements of the pest, and they may also be better suited to exploiting the invasive population if it is comprised of individuals with a genetic constitution that is most similar to those of the donor region. A CLIMEX model (Baker 2002) was parameterized with laboratory derived biological data for S. perseae (Hoddle 2002a) and used to model the distribution of *S. perseae* in the home and invaded range. CLIMEX returns an Ecoclimatic Index (EI) value that indicates the climatic suitability of particular area for a species. The larger the EI (as represented by a blue dot on the maps in Fig. 4) the better the climatic conditions for the organism of interest (Baker 2002).

Thrips specimens and associated natural enemies collected during foreign exploration were preserved in 95% ethanol and a subset of collected material was subjected to DNA analysis. The population genetics of *S. perseae* were examined using mitochondrial DNA (mtDNA) and microsatellite markers. The mtDNA sequences revealed three geographically distinct and divergent lineages, of which the mtDNA haplotypes of Californian individuals were most closely related to populations in the centre of the pest's native range. Analysis of allele frequencies at four microsatellite loci indicated Coatepec-Harinas, Mexico, as the most likely source of the Californian population. Statistically, we did not detect any bottleneck in population size associated with the invasion of California. However, estimates of the effective population size of the invading population suggest that a severe bottleneck occurred indicating that the quantity of host plant material entering California was small. Our findings implicate Coatepec-Harinas, a large avocado germplasm and breeding centre, as the most
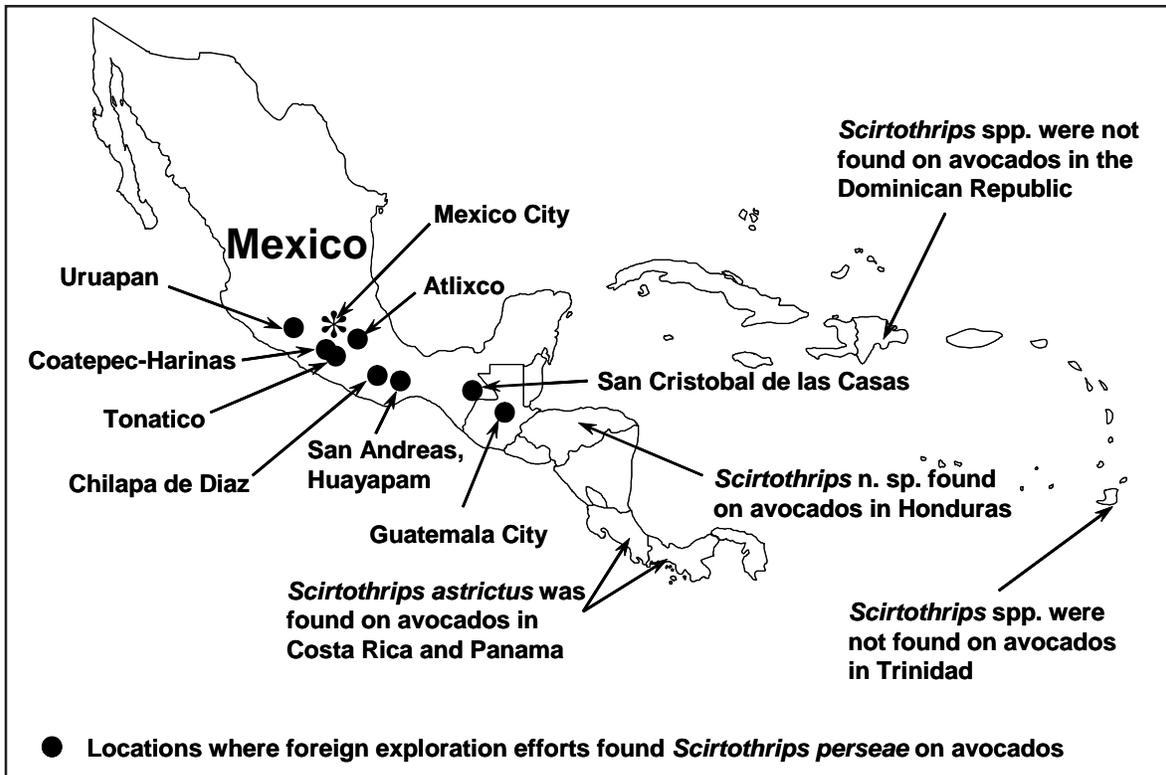
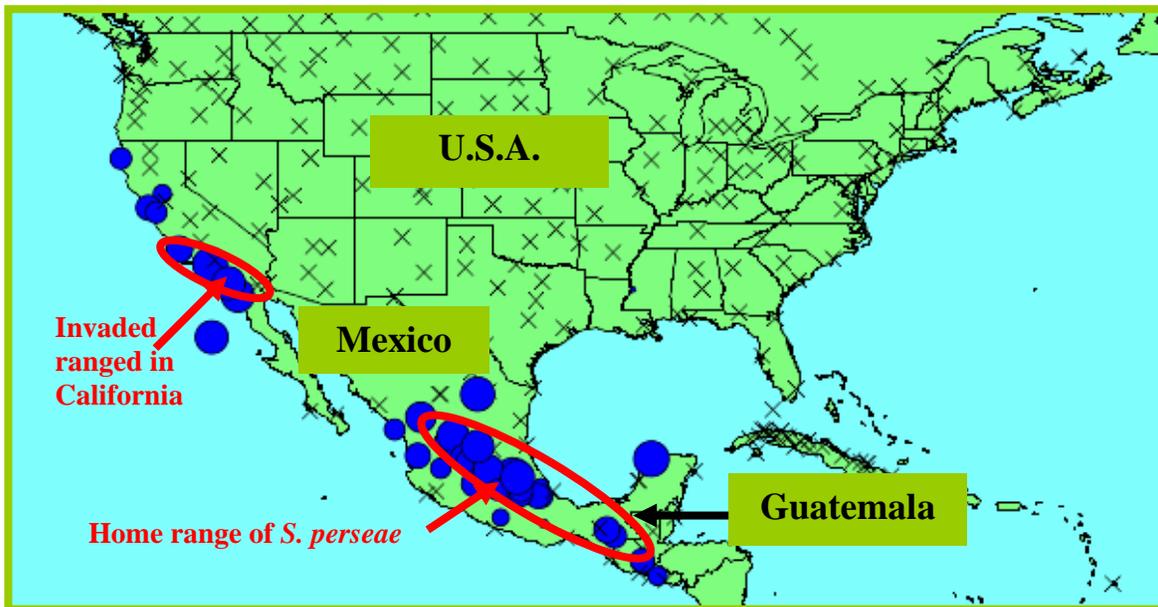**Figure 3**. The distribution of *Scirtothrips perseae* in Mexico and Central America.

Figure 4. CLIMEX predictions for the distribution for the distribution of *Scirtothrips perseae* in Mexico and Guatemala, and the invaded range in California. Crosses indicate areas that are climatically unsuitable for *S. perseae*. California is the only state in the continental U.S. that has a climate suitable for *S. perseae* populations.

likely source of the introduced Californian population of *S. perseae*, and that just one invasion event into California occurred (Rugman-Jones *et al.* 2005).

FOREIGN EXPLORATION STEP III: COLLECTING NATURAL ENEMIES FOR IMPORTATION AND EVALUATION

Our genetic analyses strongly suggest that the *S. perseae* population that colonized California originated from an area around Coatepec-Harinas in Mexico implying that natural enemies well adapted to the California haplotype of *S. perseae* should be found in this region. Further, CLIMEX indicates a very good climatic match for this area of Mexico with infested avocado growing regions in California. Future foreign exploration for host-specific natural enemies of *S. perseae* for importation into quarantine for evaluation for release in California should be focused around Coatepec-Harinas as it will likely yield natural enemies adapted to both the climate in California and the pest haplotype.

DISCUSSION

Foreign exploration is a critical element of classical biological control and it is a well accepted fact that projects have either failed or been severely impeded by importing and releasing natural enemies that are either poorly adapted to the climate in the receiving area (Van Driesche and Hoddle 2000) or fail to perform adequately on the pest biotype against which they are released (Hufbauer 2002). Given the high level of cost associated with prospecting for natural enemies overseas, the difficulty in extracting and translocating material from one country to another, and the time consuming and anxiety ridden chore of establishing viable colonies in quarantine, as much preliminary work as possible should be conducted to ensure that the best adapted natural enemies for use against the target are found and imported. Further, as momentum steadily gains towards mandatory host-specificity testing, resources can not afford to be wasted on evaluating natural enemies that may not be the most efficacious when released in the field. Setbacks of this nature should they occur may delay programs by several years as momentum is again built to commence overseas prospecting, or the program may be shut down either due to a lack of funds or based on the possibly incorrect assumption that no effective natural enemies exist for use against the target.

When compared to the "success rate" for biological control of terrestrial weeds, successful suppression of arthropod pests with natural enemies appears to be approximately 3x lower (~10% vs. ~30%) (Gurr *et al.* 2000; Syrett *et al*. 2000). One possible reason for this difference in measured success could come from the amount of preliminary prospecting in the targets home range and follow up screening and testing in quarantine before release. Typically, natural enemies used for weed control are subjected to much higher levels of scrutiny than arthropod natural enemies before release. The time from inception to release of weed natural enemies is around three scientist years at an average cost of approximately $0.5 million per agent (McFadyen 1998). In some instances, it may take up to 20 scientist years for a successful weed biological control program to be realized (Pemberton 2002). This level of effort in selecting natural enemies for release may in part explain why weed biological control programs have more successful than those for arthropods – weed programs by legislative

necessity has resulted in careful selection of targets and thorough preliminary work on identifying the important key players within the weed's home range. In fact, climate matching and genetic analyses of target populations in the invaded range are becoming routine for weed programs to facilitate the collection of agents from the same strain within the historic home range (McFadyen 1998).

Similar economic data for costs of arthropod biological control programs for comparison to weed programs are difficult to locate. However, I think it is accurate to state that historically less attention and money has been devoted to screening and evaluating arthropod natural enemies when compared to weed natural enemies. As a consequence of increased testing of natural enemies in Australia, the cost per agent has increased by 80% and the number of projects has decreased by around 30% (Van Driesche and Hoddle 1997). Greater scrutiny of arthropod natural enemies under an evolving framework of host specificity testing theory and protocols may ultimately increase not only the safety of programs, but also the efficacy because targets will need to be selected more carefully to ensure likelihood of success, and greater attention will be given to identifying promising candidates because of an economic need to eliminate at an early stage those agents with little control potential.

As illustrated here with the *S. perseae* biological control project, preliminary steps in this foreign exploration project clearly delineated the target's home range and identified the donor region within the home range of the pest. It is suggested that this type of groundwork is required to maximize success of an arthropod biological control program before expensive foreign exploration is undertaken with the intention of importing life material for evaluation in quarantine. Matching the climate of the invaded range to areas within the pest's home range is standard practice. Even greater resolution of the donor region within the home range can be achieved with genetic analyses. Haplotyping of target arthropod populations in the invaded and home range for a classical biological control program may become a standardized first step in a new project, akin to another basic first step such as climate matching. This molecular assessment as requisite preliminary step in a biological control program will not only aid in selection of natural enemies most adapted to the genetic strain(s) in the invaded range but would also identify taxonomic problems, possible cryptic species complexes, as well as indicating possible conduits by which invaders are moving. Molecular tools are promising to provide quickly and cheaply resolution to questions concerning species identity and strains or biotypes of invasive species targeted for classical biological control.

REFERENCES

Baker, R. H. A. 2002. Predicting the Limits to Potential Distribution of Alien Crop Pests. *In* Invasive Arthropods in Agriculture Problems and Solutions (G. J. Hall and C. P. Schwalbe Eds), pp. 207-241. Science Publishers Inc., Enfield.

Barlow, N. D., and Goldson, S. L. 2002. Alien Invertebrates in New Zealand. *In* "Biological Invasions Economic and Environmental Costs of Alien Plant, Animal, and Microbe Species" (D. Pimentel, Ed), pp. 195-216. CRC Press, Boca Raton.

35

Gurr, G. M., Barlow, N. D., Memmott, J., Wratten, S. D., and Greathead, D. J. 2002. A History of Methodological, Theoretical and Empirical Approaches to Biological Control. *In* Biological Control: Measures of Success (G. Gurr and S. Wratten, Eds), pp. 3-37. Kluwer Academic Publishers, Dordrecht.

Hoddle, M. S. 2002a. Developmental and reproductive biology of *Scirtothrips perseae* (Thysanoptera: Thripidae): a new avocado pest in California. *Bulletin of Entomological Research* **92**, 279-285.

Hoddle, M. S. 2002b. Oviposition preferences of *Scirtothrips perseae* Nakahara (Thysanoptera: Thripidae) in southern California avocado orchards. *Pan Pacific Entomologist* **78**, 177-183.

Hoddle, M. S., Morse, J. G., Phillips, P. A., Faber, B. A., and Jetter, K. M. 2002. Avocado thrips: new challenge for growers. *California Agriculture* **56**, 103-107.

Hoddle, M. S. 2003. Phenology of *Scirtothrips perseae* Nakahara (Thysanoptera: Thripidae) and associated natural enemies in southern California avocado orchards. California Avocado Society Yearbook 2002-2003 86, 127-145.

Hoddle, M. S. 2004a. Biological Control in Support of Conservation: Friend or Foe? In Experimental Approaches to Conservation Biology (M. S. Gordon and S. M. Bartol Eds), pp. 202-237. University of California Press, Berkeley.

Hoddle, M. S. 2004b. Restoring balance: using exotic species to control invasive exotic species. *Conservation Biology* **18**, 38-49.

Hoddle, M. S. and Syrett, P. 2002. Realizing the Potential of Classical Biological Control. *In* Invasive Arthropods in Agriculture Problems and Solutions (G. J. Hall and C. P. Schwalbe Eds), pp. 395-424. Science Publishers Inc., Enfield.

Hoddle, M. S., Jetter, K. M., and Morse, J. G. 2003. The economic impact of *Scirtothrips perseae* Nakahara (Thysanoptera: Thripidae) on California avocado production. *Crop Protection* **22**, 485-493.

Hufbauer, R. A. 2002. Evidence for nonadaptive evolution in parasitoid virulence following a biological control introduction. *Ecological Applications* **12**, 66-78.

Louda S. V. and Stiling, P. 2004. The double-edged sword of biological control in conservation and restoration. *Conservation Biology* **18**, 50-53.

McFadyen, R. E. C. 1998. Biological control of weeds. *Annual Review of Entomology* **43**, 369-393.

Nakahara, S. (1997) *Scirtothrips perseae* (Thysanoptera: Thripidae), a new species infesting avocado in southern California. *Insecta Mundi* **11**, 189-192.

Pemberton, R. W. 2002. Selection of Appropriate Future Target Weeds for Biological Control. *In* Biological Control of Invasive Plants in the Eastern United States (R. Van Driesche, B. Blossey, M. Hoddle, S. Lyon, and D. Readon Eds), pp. 375-386. USDA-ARS Forest Health Technology Enterprise Team, Morgantown, West Virginia.

36

Pimentel, D., lach, L., Zuniga, R., and Morrison, D. 2002. Environmental and Economic Costs Associated with Non-Indigenous Species in the United States. *In* "Biological Invasions Economic and Environmental Costs of Alien Plant, Animal, and Microbe Species" (D. Pimentel, Ed), pp. 285-303. CRC Press, Boca Raton.

Rugman-Jones, P. F., Hoddle, M. S., and Stouthamer, R. 2005. Population genetics of *Scirtothrips perseae*: tracing the origin of a recently introduced exotic pest of Californian avocado orchards, using mitochondrial and microsatellite DNA markers. *Molecular Ecology* (in press).

Syrett, P., Briese, D. T., Hoffmann, J. H. 2000. Success in Biological Control of Terrestrial Weeds by Arthropods. *In* Biological Control: Measures of Success (G. Gurr and S. Wratten, Eds), pp. 189-230. Kluwer Academic Publishers, Dordrecht.

Van Driesche, R. G., and Hoddle, M. S. 1997. Should arthropod parasitoids and predators be subject to host range testing when used as biological control agents? *Agriculture and Human Values* **14**, 211-226.

37

IMPACT OF INTRASPECIFIC AND INTRAGUILD PREDATION ON PREDATOR INVASION AND COEXISTENCE: CAN EXOTIC LADYBEETLES DISPLACE NATIVE SPECIES?

Paul C. J. VAN RIJN [1], Giovanni BURGIO [2], and Matt B. THOMAS [3]

[1]Netherlands Institute of Ecology (NIOO-KNAW)
Boterhoeksestraat 48
6666 GA Heteren, NL
p.vanrijn@nioo.knaw.nl

[2]DiSTA (Entomologia), Alma Mater Studiorum Università di Bologna
Viale G. Fanin 42
I-40127 Bologna, IT

[3]Department of Agricultural Sciences
Imperial College London (Wye Campus)
Wye, Ashford, Kent TN25 5AH, U.K.

ABSTRACT

Exotic predators are more likely to replace related native species when these species not only compete for similar prey species, but also predate on the offspring of the native predators. In several groups of arthropods, however, this intraguild predation (IGP) is not only mutual, but also co-occurs with intraspecific predation (ISP or cannibalism). These different processes may have counteracting effects on species invasion and coexistence. In this study, we derived simple rules that describe under which combinations of IGP and ISP a predator species is able to invade into a stable predator-prey system, and under which conditions an invasion will results in displacement or in coexistence. This theory is then applied to species pairs of exotic and native lady beetles, to test if differences in IGP and ISP may play a role in the establishment of introduced exotic ladybeetles species (Coleoptera: Coccinellidae) such as *Harmonia axyridis* in Europe and *Coccinella septempunctata* in North America. For an accurate estimation of the key processes we cannot rely on specific experimental data only, but take allometric relationships into account as well. For ladybeetles, IGP and ISP seem to be determined largely by size differences of the interacting larvae, thereby giving an overall advantage to the larger species. On the other hand, larger species generally have higher food requirements, which may give them a disadvantage in resource competition. The estimated levels of IGP, ISP and competitive ability of the interacting species can not fully explain the invasion by the two exotic ladybeetles species.

INTRODUCTION

In recent years the invasive nature of two ladybeetles (Coleoptera: Coccinellidae) has drawn considerable attention in the scientific literature. The originally Eurasian *Coccinella septempunctata* L. established and spread through the whole of North-America in the 70s and 80s (Alyokhin and Sewell 2004; Elliott *et al.* 1996). Later, in the mid 90s, the originally Asian *Harmonia axyridis* (Pallas) became established in various parts of North-America and more recently in some parts of Western Europe as well (Adriaens *et al.* 2003).

Simultaneous with their establishment in new habitats a population decline of native species was observed. The establishment of *C. septempunctata* in arable fields in North America was followed by a dramatic decline of several native ladybeetles (including *Adalia bipunctata* L.) in these fields (Alyokhin and Sewell 2004; Elliott *et al.* 1996; Evans 2004; Wheeler and Hoebeke 1995). *C. septempunctata* also became the dominant ladybeetle species in apple orchards, pushing *A. bipunctata* to a second position (Brown 2003; Brown and Miller 1998). The later establishment of *H. axyridis* in orchards resulted in a local decline of especially this other exotic *C. septempunctata* (Brown 2003), but this pattern is not yet apparent in arable fields (Nault and Kennedy 2003). In none of the cases the exotic species has resulted in the exclusion of native species.

Resource competition for aphid prey is a possible explanation for the decline in native species following the establishment of the exotic one (Evans 2004). However, no evidence is yet provided that the exotic species are better resource competitors than the native ones.

Intraguild predation (IGP) between the exotic and native ladybeetles is regarded as the most likely reason for the spread of the exotic species and the subsequent reduction of native or earlier-established species (Yasuda and Ohnuma 1999). Lab studies indeed show that the IGP by the exotic species on native species is generally bigger than the reverse predation (Snyder *et al.* 2004; Yasuda *et al.* 2004), and that IGP between the two exotic species is in favour of *H. axyridis* (Yasuda and Ohnuma 1999).

A complicating factor is that these predators not only feed on the juveniles of other predator species, but also on those from their own species. This cannibalism or Intraspecific Predation (ISP) may partly reduce the effect of IGP on population dominance.

In this study we therefore start with reviewing the theory on the combined impact of IGP and ISP on population dynamics. Then we show how the strength of the different inter- and intraspecific interaction may be calculated, and use these values to derive predictions on invasibility and species coexistence. In the second part we include resource competition in our theory. How will the various coccinelids differ in competitive ability, and how will this alter our conclusions. Finally, we will discuss the realism of our simplifying assumptions, indicate how spatial and temporal avoidance, resource partitioning and metapopulation dynamics may affect our conclusions.

39

IMPACT OF IGP AND ISP ON INVASION AND COEXISTENCE

THE MODEL

In order to derive simple rules on how IGP and ISP affect the chance that an exotic predator can invade a habitat and eventually replace native guild members, we consider pairs of predators that feed on the same prey and that are equal in their ability for resource competition, i.e. have equal functional and numerical responses. The occurrence of IGP and ISP is very stage-dependent, with the smaller juveniles falling victim by older and bigger stages, which requires a stage-structured predator-prey model. The simplest version has two stages only, with only the juvenile stage vulnerable for predation, with both stages feeding, and the adult stage reproducing. The strength of IGP and ISP (c_{xx}) is expressed as the attack rate on intraguild and intraspecific juveniles relative to that on the basic (aphid) prey (see Fig. 1).
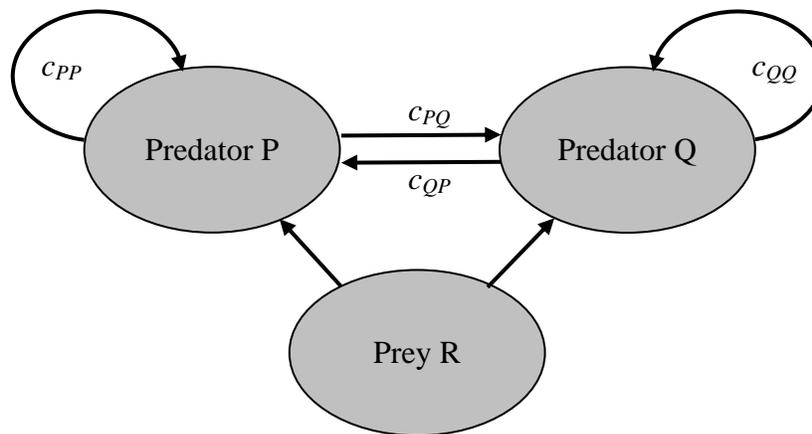

Figure 1. Food web diagram of system studied in this paper. Arrows indicate flow of biomass. Symbols show the parameters used to indicate the strength of intraspecific and intraguild predation (attack rate) relative to predation on the basic prey (resource) *R*.

In the presence of basic prey the feeding on other predators is reduced, and the reverse, according a two-prey version of Holling's disk equation (Hassell 1978). The conversion of intraguild and cannibalistic prey into predator offspring is important as well, and expressed relative to that of the basic (aphid) prey (ϕ_x).

Invasibility is studied under the assumption that a system of one predator and its prey is in equilibrium, and the question is answered: can the other predator, when still at low numbers, invade this system? When predator Q can invade a system with predator P, and predator P can invade a system with predator Q, the two predators can coexist on the same prey. By this approach the parameter conditions that allow for invasion or coexistence can be derived analytically (see van Rijn and Thomas 2005), and are shown in Fig. 2. Figure 2 shows that in absence of cannibalism no coexistence is possible. At increasing levels of cannibalism, especially when performed by both species, a wider range of IGP values leads to coexistence.
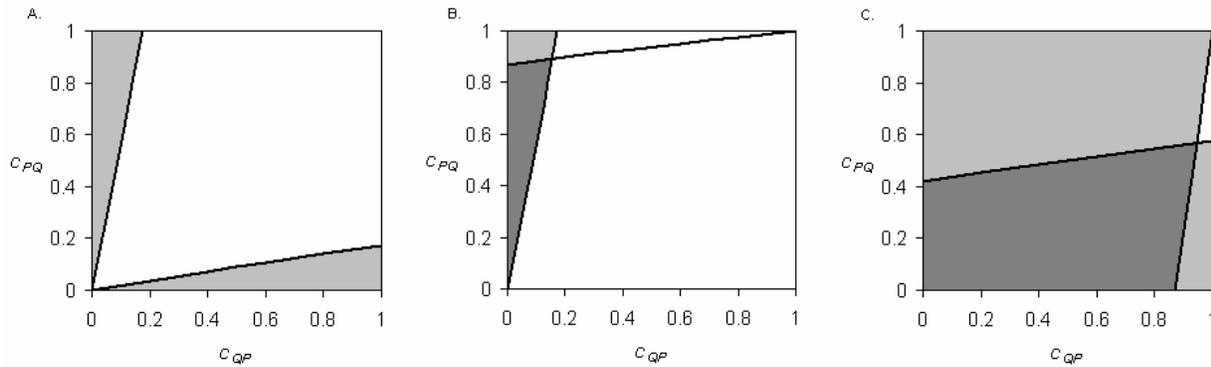
Figure 2. Mutual invasibility plots in IGP space (c_{PQ} indicates strength of IGP by species P on species Q) for different levels of ISP. A. No ISP ($c_{PP}=0$, $c_{QQ}=0$). B. ISP in P only ($c_{PP}=1$, $c_{QQ}=0$). C. ISP in both P and Q ($c_{PP}=0.5$, $c_{QQ}=1$). Light grey areas indicate IGP parameter combinations at which one species can invade the other, and dark grey areas indicate parameter combinations at which both species can mutually invade the other (allowing coexistence of P and Q).

ESTIMATING ISP AND IGP IN COCCINELLIDS

In this study we choose to focus on three species: *H. axyridis* (exotic), *C. septempunctata* (exotic in America, native in Europe), and *A. bipunctata* (native, common in America and Europe).

Experimental studies on IGP and ISP have focussed, for practical reasons, on interactions between one or two stage combinations, such as L3 - L4 (Snyder *et al.* 2004) or L2 - L2 and L2 - L4 (Yasuda *et al.* 2004). For a proper estimation of the interaction strength between the two populations all possible stage combinations should be considered. To fill this omission we utilize the commonly observed pattern that, apart for species specific effects, size difference between the two combatants strongly determine the outcome. A logistic function is fitted to the observations and used to extrapolate to unstudied interactions on the basis of the size ratio of the interaction larvae. Feeding on eggs and pupae is not considered size dependent. Conspecific eggs are strongly preferred (by all stages) over heterospecific eggs, party as a result of toxins (Agarwala and Dixon 1992). Feeding on pupae is assumed to be negligible (Schellhorn and Andow 1999). The overall intraguild or intraspecific predation rate is calculated as the mean of all the stage combinations weighed by their relative contributions to a stable population, i.e. weighed by the stage durations (including the non feeding stages, such eggs and pupae). The results of these estimations are, relative to the predation rate on aphid prey, presented in Table 1. *C. septempunctata* clearly show lower levels of cannibalism than the other species, but take intermediate positions regarding IGP (Kajita *et al.* 2000; Yasuda *et al.* 2001).

The overall conversion efficiency of cannibalistic and intraguild prey relative to aphid prey (f_x) is expected to be somewhat higher for *H. axyridis* than for the other species (Michaud and Grant 2003; Yasuda and Ohnuma 1999), but is not varied between species, and is assumed to equal 1. Other parameters (assumed to be equal for all predators) are based on the life history and predation data of *A. bipunctata* and *Myzus persicae* (Burgio *et al.* 2002; Lanzoni *et al.* 2004) and have only minor impacts on the invasion boundaries.

41

Table 1. Parameter (*c*) estimations for ISP and IGP for three coccinellid species and their combinations. *R** (critical resource density) estimations based on size; lower value indicates higher competitive ability.

Adult size (mm)	Predator	c-value, Victim			R* (relative to *h*)
		Ab	*Cs*	*Ha*	
4.5	*A. bipunctata*	0.32	0.25	0.19	0.26
7	*C. septempunctata*	0.35	0.22	0.25	0.39
8	*H. axyridis*	0.39	0.35	0.51	0.45

PREDICTIONS

The preceding theory and the given parameter estimations predict different outcomes for each of the three combinations of coccinellid predators, as shown in Fig. 3. *C. septempunctata* is able to invade a system with the native *A. bipunctata*. But since *A. bipunctata* is not able to invade a system with *C. septempunctata*, *C. septempunctata* will gradually displace *A. bipunctata*. *H. axyridis* is also able to invade a system with *A. bipunctata*, but reversely as well, so that the two species can coexist. Finally, the exotic *H. axyridis* may be able to invade a system with *C. septempunctata*, but this is uncertain, as the point is close to the invasion boundery. Since *C. septempunctata* is able to invade *H. axyridis*, the interaction will not result in its full displacement.

That, according to these calculations, *H. axyridis* will not displace *A. bipunctata* whereas the less aggressive predators *C. septempunctata* will, results from the relatively high level of cannibalism in *H. axyridis*, which, as shown before, creates room for coexistence.
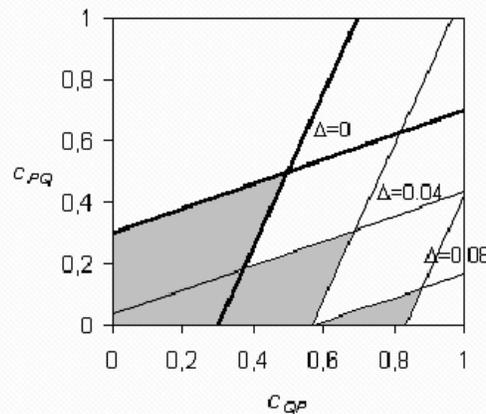

Figure 3. Mutual invasibility plot for unequal predators, based on linear functional responses. Difference in resource utilisation (*R**) between predator species is indicated by Dð, which is positive when in the advantage of *P*. IGP parameter combinations that allow for species coexistence are represented by the shaded area below and left of the two invasion bounderies. ISP levels are assumed to be moderate ($c_{PP} = c_{QQ} = 0.5$).

IMPACT OF RESOURCE COMPETITION

MODEL EXTENSIONS

Under well-mixed conditions and in absence IGP or other types of interference, the outcome of competition is predicted by Tilman's R^* rule (Tilman 1982). This rule says that the species that can maintain an equilibrium population at a lower resource (or prey) density (R^*) than other species, will outcompete these other species. Since at equilibrium reproduction equals mortality, these R^* levels result from the way reproduction and mortality is affected by prey density, i.e. the numerical response. When differences in competitive ability (differences in R^*) are incorporated in the preceding theory, the results become much more complex (see van Rijn and Thomas 2005). The basic impact, however, can be shown graphically, see Fig. 3. Increasing the competitive differences between the two predators will shift the different invasion boundaries on one direction. The positive parameter domain that allow for coexistence will consequently shrink and will ultimately become nonexistent.

ESTIMATING COMPETITIVE ABILITY IN COCCINELLIDS

Studies on the functional and numerical response of coccinellids are generally too sparse and variable to quantify differences between species. To overcome this gap in experimental data, we draw on the theory of allometric relations. The relative uniformity within the group of aphidophagous ladybeetles makes us expect that differences in prey consumption and utilisation will to a large extent result from the differences in their sizes (Dixon 2000).

Critical for the position of R^* is the shape of the functional response, and especially its half-saturation density (h). This parameter can be seen as prey handling rate divided by effective search rate. Since both these parameters should similarly scale with size, h is therefore expected to be largely independent of predator size (Gurney and Nisbet 1998). The scaling parameters of other critical parameters were estimated by analysing published data on Coccinellidae (see also Dixon 2000; Sabelis and van Rijn 1997). We estimated that maximum consumption rate and basal maintenance rate scales with length to the power 1.5 and 2.3 respectively, resulting in a scaling parameter for reproduction of 1.3.

Given the dependency of the prey equilibrium these parameters (van Rijn *et al.* 2002), R^* will increase with predator size, indicating that smaller species are better competitors. Another conclusion is that bigger species require a higher level of food supply than smaller ones to survive, which is confirmed by experiment. The study by Giles *et al.* (2002) shows that to obtain similar levels of survival *C. septempunctata* requires a higher level of food supply than the smaller *Hippodamia convergens*. The comparative studies by Obrycki *et al.* (1998) and Yasuda and Kimura (2001) show that at low prey supply the starvation related mortality of *C. septempunctata* and H. *axyridis* is much higher than of the smaller *Coleomegilla maculata* or *Propylea japonica*.

43

PREDICTIONS FOR EXOTIC AND NATIVE COCCINELLIDS

Based on the scaling rules we calculated species specific values for the critical parameters in the model (consumption rate and basal maintenance rate, together defining reproduction rate). The resulting critical (or equilibrium) prey density, R*, is indicated in Table 1.

These size-related differences in resource utilisation between the various coccinellid species do affect the predictions for invasion and coexistence, as shown in Fig. 4. The higher competitive ability of *A. bipunctata* now shifts the invasion boundary downward, so that *C. septempunctata* is no longer able to invade the system. The same is true for *H. axyridis*. In the latter case *A. bipunctata* is even able to invade a system with *H. axyridis*. In the interaction between *H. axyridis* and *C. septempunctata* it is more clear that *C. septempunctata* should win the competition.
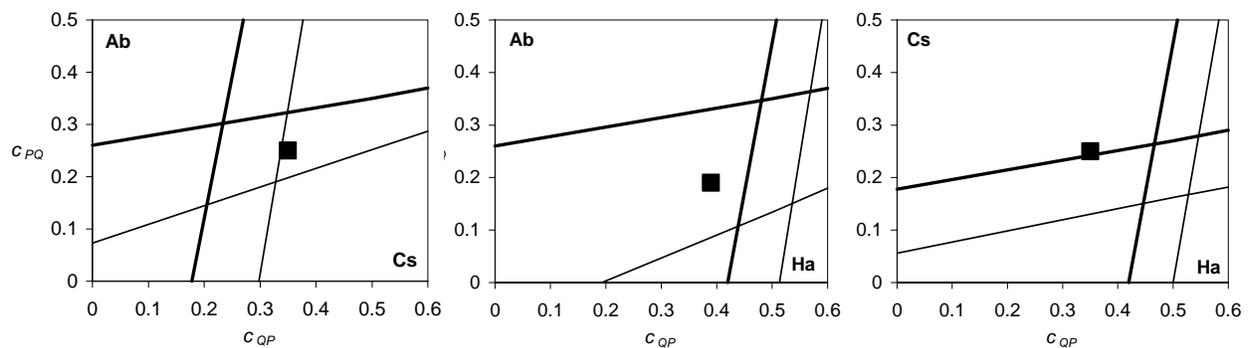

Figure 4. Mutual invasibility plots for specific coccinellid interactions, based on type II functional responses. Thick line indicates the invasion boundaries based on equal competitive abilities; thin line based on the assumption that smaller species are better competitors. Horizontal lines when native species is resident; vertical lines when exotic species is resident. See Table 1 for parameter values.

DISCUSSION

The model approach outlined above should be seen as a first step in analysing the contribution of IGP and ISP to invasion and species coexistence, taking only a few aspects of coccinellid biology into account. More general, however, the analysis shows that knowledge on the asymmetry in IGP is not sufficient to draw conclusions on the ability of a species to invade an existing predator-prey system and to displace the original predator. The level if IGP should, first of all be compared with the level of ISP. When the latter is higher than the former, the level of IGP may be sufficient to invade, but not to replace the other predator. Secondly, competition for common resources may be equally important for the outcome of the interaction. Whereas size generally is an advantage in direct interactions such as IGP, it may be a disadvantage in resource competition. Resource competition, however, can be affected by much more aspects than size, including prey specialisation, habitat dependent foraging efficiency, etc.

44

_____
Second International Symposium on Biological Control of Arthropods

ADDITIONAL MECHANISMS FOR COEXISTENCE

Without the impact of resource competition the analysis can be seen as a worst case scenario regarding species replacement, since adding more realism and complexity into that system is likely to increase the likelihood of species coexistence.

SPATIAL AVOIDANCE OF COMPETITION

Intraguild predators may perform behavioural responses that reduces the intraguild interactions. On the other hand, avoidance of intraspecific predation and competition is likely to occur as well. Larval tracks of conspecific ladybirds are known to deter ovipositing females (Yasuda *et al.* 2000). Sibling and kin discrimination by ladybird larvae and females (Joseph *et al.* 1999; Osawa 1992) may reduce ISP as well.

RESOURCE PARTITIONING

All the coccinellid predators and especially the invasive exotics, can feed on a wide range of aphid species, as well as lepidopterans, psyllids, and even pollen (Dixon 2000). Those food ranges, as well as the host plant ranges, may not fully overlap between the different species, which clearly reduces the level of competition, as well as IGP.

TEMPORAL VARIATION

Differences in time of emergence from the overwintering stage may create temporal segregation of resource utilisation. It may, however, also enhance or reverse the asymmetry in competition and IGP, as early arrivals at a resource patch have a headstart in prey depletion, and may benefit from a size advantage in direct intraguild interactions as well (Yasuda *et al.* 2004).

METAPOPULATION DYNAMICS

Finally, asynchrony in prey patch depletion, recreation and recolonisation by predators (as part of a metapopulation process) may provide additional room for coexistence when the best competitor is not the fastest coloniser as well (Osawa 2000).

REFERENCES

Adriaens, T., Branquart, E., and Maes, D. 2003. The multicoloured Asian ladybird *Harmonia axyridis* Pallas (Coleoptera : Coccinellidae), a threat for native aphid predators in Belgium? *Belgian Journal of Zoology* **133**, 195-196.

Agarwala, B. K., and Dixon, A. F. G. 1992. Laboratory study of cannibalism and interspecific predation in ladybirds. *Ecological Entomology* **17**, 303-309.

Alyokhin, A., and Sewell, G. 2004. Changes in a lady beetle community following the establishment of three alien species. *Biological Invasions* **6**, 463-471.

Brown, M. W. 2003. Intraguild responses of aphid predators on apple to the invasion of an exotic species, *Harmonia axyridis. Biocontrol* **48**, 141-153.

45

Brown, M. W., and Miller, S. S. 1998. Coccinellidae (Coleoptera) in apple orchards of eastern West Virginia and the impact of invasion by *Harmonia axyridis*. *Entomological News* **109**, 143-151.

Burgio, G., Santi, F., and Maini, S. 2002. On intra-guild predation and cannibalism in *Harmonia axyridis* (Pallas) and *Adalia bipunctata* L. (Coleoptera : Coccinellidae). *Biological Control* **24**, 110-116.

Dixon, A. F. G. 2000. "Insect Predator-Prey Dynamics: Ladybird Beetles and Biological Control". Cambridge University Press, Cambridge, U.K.

Elliott, N., Kieckhefer, R. and Kauffman, W. 1996. Effects of an invading coccinellid on native coccinellids in an agricultural landscape. *Oecologia* **105**, 537-544.

Evans, E. W. 2004. Habitat displacement of North American ladybirds by an introduced species. *Ecology* **85**, 637-647.

Giles, K. L., Madden, R. D., Stockland, R., Payton, M. E., and Dillwith, J. W. 2002. Host plants affect predator fitness via the nutritional value of herbivore prey: Investigation of a plant-aphid-ladybeetle system. *Biocontrol* **47**, 1-21.

Gurney, W. S. C., Nisbet, R.M. 1998. "Ecological Dynamics". Oxford University Press, Oxford, U.K.

Hassell, M. P. 1978. "The Dynamics of Arthropod Predator-Prey Systems". Princeton University Press, Princeton, NY.

Joseph, S. B., Snyder, W. E., and Moore, A. J. 1999. Cannibalizing *Harmonia axyridis* (Coleoptera : Coccinellidae) larvae use endogenous cues to avoid eating relatives. *Journal of Evolutionary Biology* **12**, 792-797.

Kajita, Y., Takano, F., Yasuda, H., and Agarwala, B. K. 2000. Effects of indigenous ladybird species (Coleoptera : Coccinellidae) on the survival of an exotic species in relation to prey abundance. *Applied Entomology and Zoology* **35**, 473-479.

Lanzoni, A., Accinelli, G., Bazzocchi, G. G., and Burgio, G. 2004. Biological traits and life table of the exotic *Harmonia axyridis* compared with *Hippodamia variegata*, and *Adalia bipunctata* (Col., Coccinellidae). *Journal of Applied Entomology* **128**, 298-306.

Michaud, J. P. and Grant, A. K. 2003. Intraguild predation among ladybeetles and a green lacewing: do the larval spines of *Curinus coeruleus* (Coleoptera : Coccinellidae) serve a defensive function? *Bulletin of Entomological Research* **93**, 499-505.

Nault, B. A. and Kennedy, G. G. 2003. Establishment of multicolored Asian lady beetle in Eastern North Carolina: Seasonal abundance and crop exploitation within an agricultural landscape. *Biocontrol* **48**, 363-378.

Obrycki, J. J., Giles, K. L., and Ormord, A. M. 1998. Interactions between an introduced and indigenous coccinellid species at different prey densities. *Oecologia* **117**, 279-285.

Osawa, N. 1992. Sibling cannibalism in the ladybird beetle *Harmonia axyridis* - Fitness consequences for mother and offspring. *Researches on Population Ecology* **34**, 45-55.

46

Osawa, N. 2000. Population field studies on the aphidophagous ladybird beetle *Harmonia axyridis* (Coleoptera : Coccinellidae): resource tracking and population characteristics. *Population Ecology* **42**, 115-127.

Schellhorn, N. A. and Andow, D. A. 1999. Mortality of coccinellid (Coleoptera : Coccinellidae) larvae and pupae when prey become scarce. *Environmental Entomology* **28**, 1092-1100.

Snyder, W. E., Clevenger, G. M., and Eigenbrode, S. D. 2004. Intraguild predation and successful invasion by introduced ladybird beetles. *Oecologia* **140**, 559-565.

Tilman D. 1982. "Resource Competition and Community Structure." Princeton University Press Princeton, NY.

van Rijn, P. C. J. and Thomas, M.B. 2005. Effect of intraspecific and intraguild predation on the coexistence of competing predators. *American Naturalist*, submitted.

van Rijn, P. C. J., van Houten, Y. M., and Sabelis, M. W. 2002. How plants benefit from providing food to predators even when it is also edible to herbivores. *Ecology* **83**, 2664-2679.

Wheeler, A. G., and Hoebeke, E. R. 1995. *Coccinella novemnotata* in Northeastern North-America - historical occurrence and current status (Coleoptera, Coccinellidae). *Proceedings of the Entomological Society of Washington* **97**, 701-716.

Yasuda, H., Evans, E. W., Kajita, Y., Urakawa, K., and Takizawa, T. 2004. Asymmetric larval interactions between introduced and indigenous ladybirds in North America. *Oecologia* **141**, 722-731.

Yasuda, H., Kikuchi, T., Kindlmann, P., and Sato, S. 2001. Relationships between attack and escape rates, cannibalism, and intraguild predation in larvae of two predatory ladybirds. *Journal of Insect Behavior* **14**, 373-384.

Yasuda, H., and Kimura, T. 2001. Interspecific interactions in a tri-trophic arthropod system: effects of a spider on the survival of larvae of three predatory ladybirds in relation to aphids. *Entomologia Experimentalis et Applicata* **98**, 17-25.

Yasuda, H., and Ohnuma, N. 1999. Effect of cannibalism and predation on the larval performance of two ladybird beetles. *Entomologia Experimentalis et Applicata* **93**, 63-67.

Yasuda, H., Takagi, T., and Kogi, K. 2000. Effects of conspecific and heterospecific larval tracks on the oviposition behaviour of the predatory ladybird, *Harmonia axyridis* (Coleoptera : Coccinellidae). *European Journal of Entomology* **97**, 551-553.