



# Team building in biocontrol

Prof.dr G.J. Messelink

Inaugural lecture upon taking up the position of Special Professor of Biological Pest Control in Greenhouse Production Systems at Wageningen University & Research on 28 October 2021



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Front cover image by Gerben Messelink

# Team building in biocontrol

## *An ecosystem approach in biological pest control in greenhouse cropping systems*

*Esteemed rector magnificus,*

*Dear colleagues, students, family and friends, ladies and gentlemen*

About two years ago, we went with our research team from the Business Unit Greenhouse Horticulture of Wageningen Research to a remote place in a wooded area. The place was beautiful, a former monastery with a great atmosphere, high ceilings, paintings, you could smell the history... After some drinks, good food and a good night, we were totally relaxed and open for what the day could bring us. And no, it did not bring us horse whispering, boxing or walking on fire to foster better collaboration within our team. Instead, we used a very interesting methodology to analyse the natural behavioural preferences and strengths of each team member, which were visualised in a wheel by different colours. As good scientists, we were rather sceptical about the methodology and started to discuss the value of it. Interestingly, apart from the discussion about criteria and methods, the analyses surprisingly showed a large diversity of functional traits of our team members, with all different colours being represented. Some displayed a preference for decision making, some were more analytical, some more supportive and others more creative. It was an eye-opener for me that even among scientists with the same job, it is beneficial to have such diversity within a team. The makers of this tool claim these insights will increase the self-awareness of team members and result in better relationships, as well as higher efficiency and resilience. Great!

Today in this inaugural address, I will talk about team building for biocontrol, and I see a lot of parallels with building effective teams of people in companies and research organisations. Also in biocontrol we want to increase resilience in the cropping environment with diverse assemblages of natural enemies to achieve effective results. Before I go into detail about team building for biocontrol, I would like to start with giving a bit of context. What is biocontrol and how did it start? Why is biocontrol so important for some major global challenges? And how do I plan to contribute to biocontrol development with this position as a special professor?

## The success story of biological control in greenhouses

Biological control, or biocontrol, is the exploitation of living organisms to combat pests, pathogens or weeds. These living biological control agents (BCAs) can be subdivided into different categories. There are predators, parasitoids, entomopathogens (pathogens of insects) and plant pathogen antagonists [1]. Biological pest control in greenhouse horticulture started already in the 1920's, with the English discovery and subsequent production of the parasitoid *Encarsia formosa* for the control of the greenhouse whitefly in tomato [2]. However, the enthusiasm for using biological control quickly dropped when cheap and effective pesticides became available after the second world war, and the success of the parasitoids *E. formosa* fell into oblivion [3]. The use of pesticides has thereafter dominated pest and disease control practices for several decades, and in many parts of the world this is still the case. However, the overuse of pesticides promotes the development of pesticide resistance, resulting in ineffective chemical control [4]. In addition, the removal of naturally occurring biological control agents through the adverse effects of broad-spectrum pesticides can in many cases result in pest resurgence [5]. In the late 1950's, the concerns about these adverse effects of pesticides led to the introduction of 'integrated control' defined as 'applied pest control which combines and integrates biological and chemical control' [6]. This was further boosted by the awareness of the destroying effects of pesticides on ecosystems, published in the famous book "Silent Spring" by Rachel Carson in 1962 [7]. The strong adverse impact of pesticides on the environment, food safety and the health of workers who are in direct contact with pesticides, was further revealed in later studies, for example studies that showed the impact of neonicotinoids on pollinators [8,9].

Biological control in greenhouses started again in the 1960' when spider mites (*Tetranychus urticae*) became resistant against several pesticides [10], and when the predatory mite *Phytoseiulus persimilis* was discovered as an effective spider mite control agent [11]. Severe whitefly outbreaks in the early 1970's led to the rediscovery of *E. formosa*, and improved methods for rearing and shipping this parasitoid led to an effective and widely accepted whitefly biological control programme [12]. In the 1980's, the finding that many phytoseiid predatory mites could be mass-produced on a system of bran and astigmatid prey mites was a major breakthrough, because this enabled the mass production of these predatory mites in a cheap and massive way [13]. Predatory mites mass-reared in this way nowadays play a major role in the control of thrips, spider mites and whiteflies. Since the 1990's, the development of biological control in greenhouses strongly increased with several new species of natural enemies being mass-produced and released in greenhouse crops (Figure 1). In addition to specialist natural enemies, generalist predators also became more popular because of their ability to control multiple pest species and to establish

populations in absence the pest. Right now, an estimated number of 350 arthropod and nematode BCAs are commercially available world-wide [14]. Moreover, more than 200 strains of microbial BCAs (fungi, bacteria and viruses) were registered for pest and disease management, although this is probably a large underestimation of the real number of strains used in biocontrol [14].



Figure 1. Some examples of specialist and generalist natural enemies in greenhouse crops. Left the specialist parasitoids *Aphidius ervi* and *Encarsia formosa* and right the generalist predators *Amblyseius swirskii* and *Orius majusculus*.

In general, control strategies have evolved from ‘prophylactic calendar spraying’ to the use of pesticides based on the monitoring of pest and disease damage- and action thresholds (‘threshold-based pesticide application’) towards (ecologically-based) IPM that includes multiple non-chemical methods. In this approach, pesticides, preferably compatible with natural enemies, are only used as a last option to reduce high pest densities.

Customers, retailers, and governments in many countries are nowadays concerned about the use of pesticides, resulting in the demand of pesticide residue-free products, a reduced availability of pesticides and a strong increase of biological control application.

## Major global problems

Because of the success of biological control in greenhouse crops, we are now able to produce healthy and safe vegetables and fruits. Sustainable greenhouse production can be important for some of the major global problems. We all know, we are facing the major threats of climate change and loss of biodiversity. Climate change seems to accelerate and we are increasingly experiencing the consequences, such as the recent floods in The Netherlands, Belgium, Germany and China and the incredible heat waves in Canada, the US and Siberia. Both climate change and the loss of biodiversity are threatening food production for the fast growing world population. In 2018, the Food and Agricultural Organization (FAO) of the United Nations updated her analyses of the future needs for food and agriculture to 2050 [15]. Although we know the facts, the challenge remains enormous. The world population has strongly increased over the last decades. Between the year I was born and now, the population more than doubled to an estimated size of 7.8 billion people right now. According to world population prospects of the Population Division of the Department of Economic and Social Affairs of the United Nations Secretariat, the world population growth is slowing down, but approaching 10 billion people in 2050 [16]. Moreover, on top of that, there is a large shift worldwide to urbanisation (Figure 2).

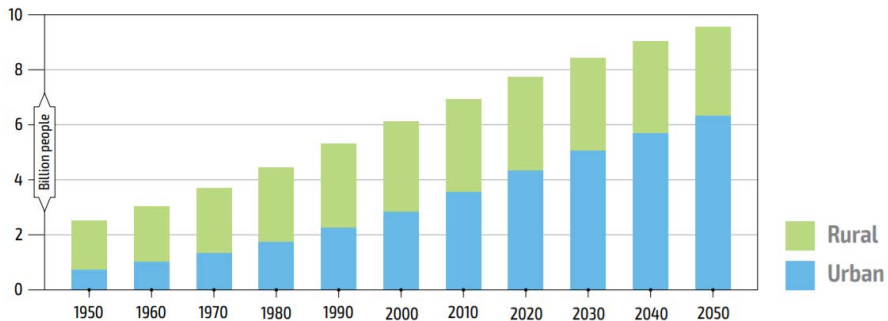


Figure 2. Global urban and rural populations: historical and projected [15]

Producing sufficient healthy food in a sustainable way for a growing world population is thus challenging. In addition, the COVID-19 pandemic also changed our view on food production world-wide. Food availability is one of the primary needs and the world-wide lock-downs showed how fragile large cities are when transport of food from outside is blocked. This awareness led to an increased wish to be more self-supporting in the production of sustainable food [17] and may result in an increased demand for local food production in urbanised areas.



I believe the greenhouse sector can play a major role in facing these challenges of climate change, biodiversity loss, urbanisation and the need for local food production. Intensification of cropping systems is needed to increase production and yield, but at the same time, inputs of pesticides, chemicals, water and energy need to be reduced to meet the requirements for sustainability. In the impressive 2020 documentary “A Life On Our Planet”, the famous Sir David Attenborough advocates the restoration of planetary biodiversity, the limitation of human population growth, a shift to renewable energy, a reduction in meat consumption, and the allocation of more areas for natural preservation. He mentioned modern greenhouse production in The Netherlands as an avenue to reach these goals. Indeed, production levels are incredibly high. Tomato yield per square meter, for example, is in Dutch modern greenhouses 13 times higher compared to the average yield worldwide (FAOSTAT). With the right design of modern greenhouses, fresh vegetable production is possible even in arid and hot climates with minimal use of water [18]. And pesticide use can in principle be very limited. A survey among Dutch greenhouse growers shows that biological control is applied in almost 100 percent of the vegetable crops (Figure 3). Also in ornamental crops the application of biological control as an alternative for pesticides is growing fast.

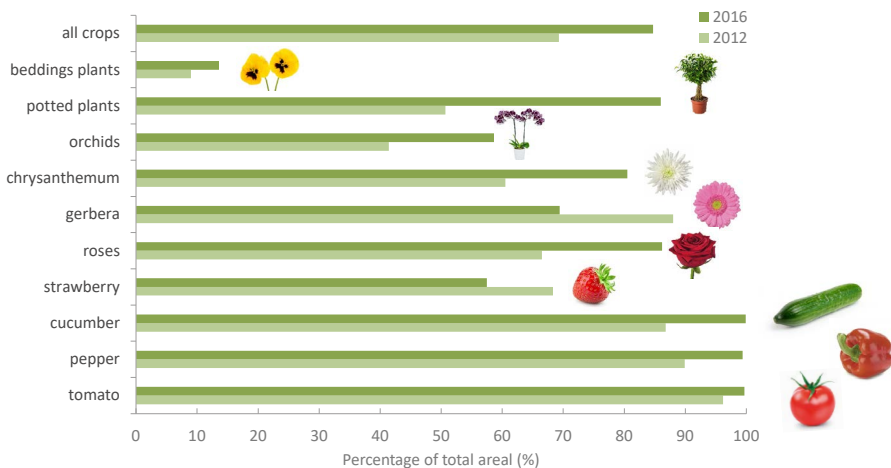


Figure 3. Application of biological pest control in the Dutch greenhouse sector (source CBS 2018).

However, pesticides are still used in almost all greenhouse crops and this use is particularly high in some ornamental crops where application reaches levels of 40 to 80 kg/ha per year (source: [www.clo.nl/nl000607](http://www.clo.nl/nl000607)).

## Challenges in Biological Pest control

Although biological control has been applied very successfully in greenhouse crops, there are still many challenges to solve. The most important reason is the continuous flow of new invasive pests that colonise greenhouse crops. The Dutch greenhouse sector is confronted almost every year with a new pest or pathogen species. This strongly disrupts the existing biological control systems when non-chemical control measures are not available. Tomato, for example, has long been the prime example of successful sustainable crop protection with minimal use of pesticides and an effective biological control system. However, in recent years the use of pesticides in tomatoes has increased again, because of the need to control the invasive pests such as the tomato russet mite *Aculops lycopersici*, the South American tomato pinworm *Tuta absoluta* and the omnivorous bug *Nesidiocoris tenuis*. In addition, there are also major problems with new viruses such as the Tomato brown rugose fruit virus ToBRFV.

Sweet pepper is another example of a crop where the biological control system has been disrupted by the arrival of an invasive pest species. Thrips and spider mites in sweet pepper were controlled very effectively by a combination of predatory bugs and predatory mites until the arrival of the southern green stink bug *Nezara viridula*. The development of new biological control agents against these invasive pests needs time, and meanwhile growers need to spray pesticides simply because no alternatives are available. The pesticides used also have strong side-effects on the natural enemies used for controlling other pests and thereby disrupt the system.

Ornamental greenhouse growers have been unpleasantly surprised by a number of invasive thrips species that are hard to control, such as the Japanese flower thrips, *Thrips setosus* and the onion thrips, *Thrips parvispinus*. Also here, new biological control solutions are urgently needed and growers shift back to chemical control when these solutions are not available.

In addition to invasive pests, pressure from indigenous pest species is also increasing. The European tarnished plant bug, for example, can make more generations during years with milder winters and hot summers and hence cause greater damage. Climate change will thus increase problems with such noxious species. Also, the reduced availability of pesticides increases problems with indigenous and established pests, such as aphids and mealybugs. Some so-called “secondary pests” can become important key pests when broad spectrum pesticides are not used anymore.

All these cases show that biological control systems continuously need adaptations to control the wide range of pests and pathogens. A major question is how to control all

the current pests and the species we can expect in the near future, in a sustainable way? Can we enhance the current biological control systems to be better prepared for future risks? Which strategies offer most perspectives?

## Team building in biocontrol

Well, I believe that the only way to control the wide range of currently occurring pests and the new invasive species we can expect in the future, is to develop resilient cropping systems. Crop resilience can be based on preventive releases and long-term establishment of natural enemies that create in that way a “standing army”, protecting the crops against new invasions of pests [19]. Several species of natural enemies are needed to control the increased diversity of greenhouse pest. Greenhouse crops offer the unique possibility to manipulate communities of natural enemies by selecting a specific array of species that are commercially available [14]. Based on the abundance, diversity and the relative risk of a certain pest species, it is possible to adapt the strategies of natural enemy releases. The main question here is: which natural enemy assemblages are the most effective for suppressing this wide variety of pests in the different cropping systems? How can we build teams that achieve the best results?

To answer these questions, it is important to consider all possible interactions among species in arthropod food webs. Which combinations of natural enemies are effective has been subject to studies for a long time, because they are potentially involved in positive or negative interactions with each other that can influence the strength of pest control. In fact, many studies indicate that trophic interactions among diverse natural enemy assemblages may result in a full spectrum of outcomes including null, additive, antagonistic or synergistic effects [20]. Detrimental effects can mainly be expected from hyperpredation or hyperparasitism, which occurs when predators or parasitoids consume another species of natural enemy without sharing the same pest as prey. Such interactions can be very disruptive for biocontrol. We found, for example, that predatory mites consume the eggs of the predatory midge *Aphidoletes aphidimyza*, thus disrupting the biological control of aphids [21]. Another potentially negative interaction is intraguild predation, which occurs when natural enemies that compete for the same prey is combined with predation by one species of natural enemy on another [22]. Predators, for example, can eat immature parasitoids developing within their prey, and thereby reduce the parasitoid impact on a pest. Studies about intraguild predation became very popular and created a huge number of scientific papers. In some cases, these interactions have indeed shown to disrupt pest control. However, many studies are too simplified and tend to overestimate the severity of these disruptive effects in more complex systems with multiple niches for both pests and natural enemies. Negative effects can be outweighed by other – positive – effects of

generalist predators [23]. I think that the potential negative interactions among natural enemy species has received disproportional attention in scientific studies and future research should focus more on the complementarity and synergy among natural enemies. From several studies it is now known that in most cases increased natural enemy richness also results in a better suppression of pests [20]. However, diversity in itself does not necessarily result in better pest control. Ecologists generally agree that diversity of functional traits, rather than species number or identities, is responsible for steering ecosystem processes. Thus there should be a functional diversity of natural enemy species through the unique way each of these species contributes to pest control. It is very interesting to study and understand the underlying mechanisms of the positive effects of natural enemy diversity on pest control, because it can help us to design more effective biological control strategies. Here I would like to discuss 5 possible mechanisms we can utilise in greenhouse biocontrol programmes.

First – and this is rather obvious – different species of natural enemies can control different species of pests. Biological control of pest species has traditionally mainly focused on specialist natural enemies, each attacking a specific pest and with this approach, natural enemy species will in most cases complement each other. In contrast, generalist predators can prey upon a wide range of pests. However, even then, it can be the case that one pest is preferred over another pest by a generalist predator. In sweet pepper, for example, we found that the combination of the generalist predatory bugs *Orius laevigatus* and *Macrolophus pygmaeus* gives the best control of thrips and aphids, in spite of their involvement in intraguild predation [24].

Second, natural enemies can complement each other by feeding on different pest stages. There is often a strong morphological and behavioural differentiation among pest developmental stages and this can promote functional complementarity among natural enemy species. A nice example in greenhouses is the control of whiteflies. Predatory mites mainly predate upon the eggs and crawlers of whiteflies, whereas the parasitoid *E. formosa* prefers to parasitise the third and fourth larval stages. Also the parasitism of leafminer larvae residing inside the leaf tissue by *Diglyphus isaea* can be perfectly combined with the predation of the last-instar larvae that emerge from the mines by predatory bug *Orius laevigatus*. This pest stage complementarity showed to enhance leafminer control in our experiments.

Third, there can be spatial complementarity between natural enemies when they prefer different habitats. Some species of predatory mites, for example, are active high in the plants and others lower in the plant, thereby complementing the control of the same pest [25]. This spatial complementarity can even occur at the small scale of a single leaf. Studies in cabbage showed that some ladybird beetles mainly forage



The fifth mechanism is predator facilitation. Natural enemy species can interact synergistically, resulting in a stronger pest suppression than expected on the individual kill rates of each natural enemy species. In other words, there are non-additive changes in resource consumption. This occurs, for example, when one predator induces prey behaviour that puts the prey at greater risk towards a second predator, or where increased diversity is associated with changes in the way prey individuals are distributed [27]. There are many examples in nature showing this synergistic multi-enemy effect on prey. I would like to show one spectacular example from the sea. Northern Gannets, which are fish-eating seabirds, dive into the ocean at high speeds when they are hunting for fish. Sometimes, they receive help from dolphins that herd the fish into dense concentrations near the surface. This clearly facilitates the predation by the sea birds from above. This phenomenon is shown in the famous BBC series Planet Earth. Similar mechanisms have been observed for predatory fish and sea snakes hunting together for small fish. Also in food webs of arthropod pests and natural enemies such synergistic interactions have been observed. A well-known example is the system where foliar-foraging ladybirds induce dropping behaviour as a defence response in aphid colonies and thereby facilitate the predation of aphids by ground-foraging carabid predators [28]. It will be interesting to explore whether such synergistic interactions among natural enemies in greenhouses exist and can be utilised to optimise pest control.

Coming back to the team member profiles for efficient team work: a similar analysis may be useful to provide insight into the specific strengths of natural enemies and the way they can complement each other to get the job done. Complementarity can arise from natural enemy species with different hunting techniques and climatic preferences that are active at different times during the day and attack different pest species or stages located in different habitats in the greenhouse. Figure 5 shows my attempt to visualise an example of this functional diversity for team work in biocontrol.

## Research lines

Summarising, my vision is that biological control in greenhouses needs to be further developed with an ecosystems approach to optimise functional diversity for maximum pest control capacity, taking into account all possible interactions within pest-natural enemy communities in relation with the greenhouse climate and the crop. A better understanding of the functioning of ecosystems in greenhouses is essential for developing and designing biological control systems. With the entomology group of the BU Greenhouse Horticulture of Wageningen Research and colleagues, MSc and PhD students of the laboratory of Entomology of Wageningen University, we work on several research lines to design and develop effective biological pest control systems and increase crop resilience.

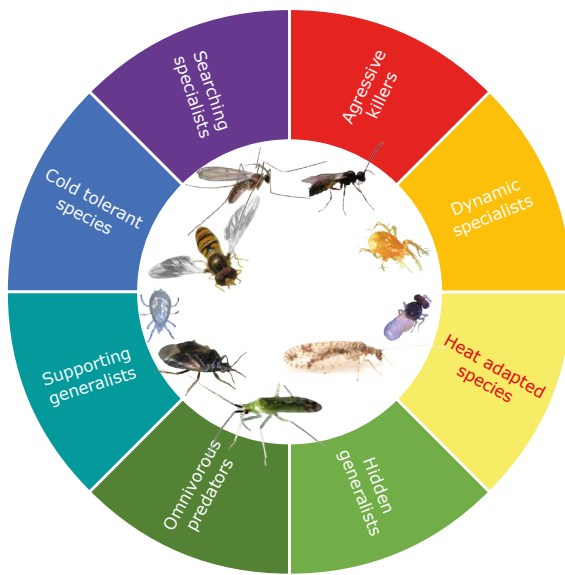


Figure 5. An attempt to visualise some of the complementarities needed for biocontrol team building.

### **New species of natural enemies**

As discussed, increasing the functional diversity of natural enemies will in general enhance pest management. Our future work will mainly focus on new species that complement existing species that are already widely used in practice. In several projects we now look for species with a different foraging behaviour, or species that are better adapted to specific climatic conditions. In many cases we focus on species that establish well at low pest densities and generalist and omnivorous predators that predate on multiple pest species and can survive on alternative food sources.

### **Supporting establishment and increasing diversity of natural enemies**

Poor establishment and persistence of natural enemies is one of the main problems in biological control. Natural enemies need alternative food sources, prey, hosts, shelter and oviposition sites to establish populations, and this is not always present in monocultures of greenhouse crops grown on artificial substrates. Biological control can be enhanced in such crops by supplementing the missing resources, such as the application of alternative food sources (pollen, *Ephestia* eggs, *Artemia* cysts), alternative prey (non-pest aphids, prey mites) and/or by providing conditions that facilitate successful establishment of natural enemies (“the standing army”) [19]. Optimising long-term establishment of natural enemy populations might also require

a new design of the greenhouse cropping systems with more diversity of plants that support specific needs of natural enemies, for example soft plant tissue for oviposition of predatory bugs or flower nectar for adult lacewings and syrphids. In these studies we also include the potential effects of functional diversity in the vegetation surrounding the greenhouses, that can support both arthropod biodiversity around greenhouses as well as natural enemy biodiversity inside greenhouses (Figure 6).

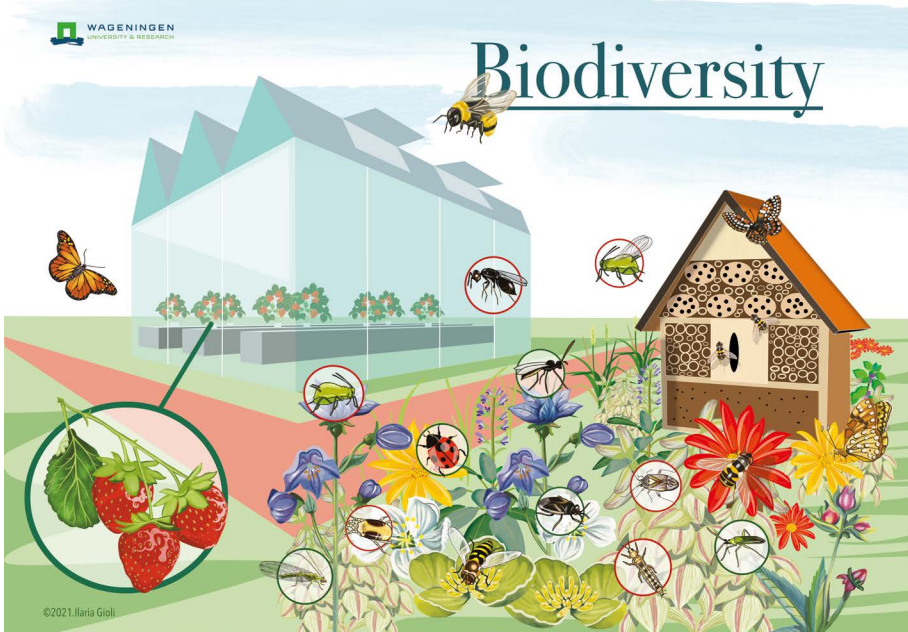


Figure 6. An impression of biodiversity around greenhouses that potentially can support biological pest control.

### Food web complexities

More natural enemies in biological control programmes also means more interactions among species which can affect pest control in an infinite number of ways [13]. Not only the diversity of natural enemies, but also the diversity of pest species and the provision of alternative food can affect biological control in both positive and negative ways. Evaluations of biological control systems under realistic greenhouse conditions with multiple pests and natural enemies is thus important to include these food web complexities. In our greenhouse studies we try to better understand these interactions and to reduce potential negative interaction such as hyperparasitism, intraguild predation and increase additive or synergistic effects by providing more



diversity of (micro)habitats in cropping systems. Modelling can help to predict the outcome of such interactions, which can afterwards be validated in greenhouse trials.

## IPM

Biological control is often part of a larger system comprising of multiple methods of pest control, also called Integrated Pest Management (IPM). For example, the use of arthropod natural enemies can be complemented by using entomopathogenic microorganisms [29] or inducing the defence mechanisms of the crop [30]. It is important to consider the possible effects on biological pest control when integrating different control methods. Ultimately, everything intertwines in greenhouse cultivation and a holistic approach is necessary to achieve pest control solutions. In many of our projects we try to look at the larger IPM system and we investigate the influence of the cultivation substrate, climate, lighting, plant traits and crop structures on biological pest control.

## Curiosity and serendipity

I strongly believe there is still so much to explore and learn from nature that we can apply in biological pest control. This all starts with an intrinsic curiosity about how systems function, and how species interact and behave. Therefore time for field work and observations is in my opinion essential and should be created in the busy time schedules of project management. Curiosity driven science may also result in serendipities, the phenomenon of finding valuable things not sought after.

Unplanned fortunate discoveries occur commonly in science, such as the discovery of penicillin in 1928 by the Scottish researcher Sir Alexander Fleming. A famous quote from Fleming is:

*“One sometimes finds what one is not looking for. When I woke up just after dawn on Sept. 28, 1928, I certainly didn’t plan to revolutionize all medicine by discovering the world’s first antibiotic, or bacteria killer. But I guess that was exactly what I did.”*

Serendipities also played an important role in the discovery of many natural enemy species. One of the early observations in The Netherlands goes back to the 17<sup>th</sup> century.

Johannes Goedhaert (Figure 7) was a painter living in the 17<sup>th</sup> century who was fascinated by the diversity of maggots, worms, caterpillars and all kinds of larvae he found in nature. He kept them in pots and bottles and tried to feed them with their natural food sources like plant leaves and observed some magic changes that seemed so far to be unknown. Ugly larvae changed into beautiful butterflies and maggots into pupae and flies. He published his observations after 25 years of work in the

famous book “*Metamorphosus Naturalis*” that was released in 1670 [31], and he is now considered to be the discoverer of the metamorphosis of insects.



Figure 7. Johannes Goedaertius (1617-1668), painted by Reinier van Persijn

Very interestingly, among the descriptions of metamorphosis, Johannes Goedaertius also described some cases of insects preying on other insects. He observed for example syrphid flies laying eggs in aphid colonies and the larvae preying on aphids (Figure 8). He also described the remarkable furtive behaviour of syrphid larvae in aphid colonies. Funnily enough, he named these insects “sluggards” (*luiaards*), because most of the time these larvae appear to be dead or sleeping. However when active, they carefully approach aphids, quickly attack and suck the aphids empty. Nowadays we know these larvae are very important natural enemies for aphid control and this observed furtive behaviour prevents migration in aphid clusters. Without knowing and understanding, he also described several cases of parasitism of caterpillars. He was very surprised that the same species of caterpillars could result in one case in a beautiful butterfly and in another case in the emergence of several flies (Figure 8).

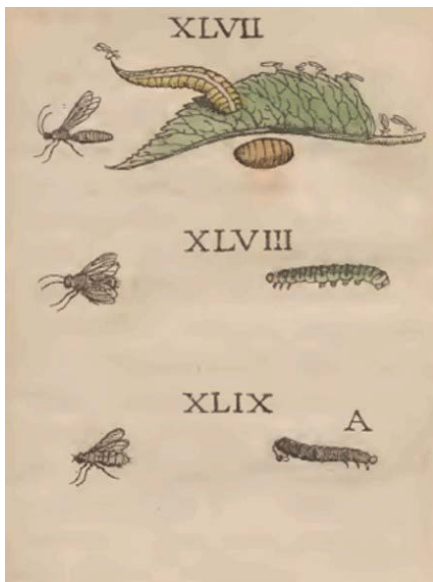


Figure 8. Syrphid larvae feeding on aphids (left) and parasitism of the larval stages of *Nymphalis polychloros* (right).

Although Goedhaert already mentioned that insects are largely overlooked and should be studied in more detail, he probably would never have realised that what he observed, now plays an incredibly important role in sustainable food production worldwide. Observations like these are still needed to understand species interactions and to come up with new ideas for biological pest control.

## Cooperation

Studies on team building in biocontrol also requires team building in research. Complementarity among scientists with different fields of expertise is essential to solve complex problems and develop innovations. Wageningen University and Research is a great environment for this multidisciplinary approach in research, which ranges from fundamental to very applied research. With my position as a special professor in biological pest control at the Laboratory of Entomology, I hope to strengthen the connection between basic and applied research. In my other position, in the entomology group at the Business Unit Greenhouse Horticulture of Wageningen Research, I am more involved in applied research projects in biological control. This offers a great opportunity to connect MSc students to applied projects in the greenhouse sector and to strengthen applied research with more fundamental PhD-projects about biological pest control.

The willingness to share ideas and have open and stimulating discussions among scientists is extremely important for research and I believe that trust and friendship is required for that. This is why physical project meetings and conference visits are so important. I know we live in a competitive world and there can be conflicting interests among scientists or industries, but eventually we all work on the same goal to increase the sustainability of the agricultural sector, which connects us deeply.

A close relationship and collaboration with growers, consultants and the biological control companies is also essential for developing biological control systems that can be applied in reality. During my career, I have learned so much from growers and consultants that practice biological control every day. I also have a deep respect for all the growers that have been willing to take the risks to reduce pesticide use and try new approaches in biocontrol, which sometimes involved huge crop losses. A close connection with practice is of great importance to identify the knowledge gaps and prioritise research programmes for biological control.

## Education

Wageningen University is internationally well-known and ranked as the best agricultural university world-wide. Currently, 20% of the more than 13000 students are international, coming from more than 100 different countries. This offers great opportunities to teach and inspire new students from all over the world about biological pest control, knowledge they can apply afterwards in their own countries. This is more than ever needed for producing food and flowers in a sustainable way. New generations of students will also be important to further develop novel approaches in biological control. With the special chair for biological control in greenhouse production systems, I will contribute to education through courses about biological pest control and by supervising MSc and PhD students. I hope we can inspire students in the existing biological control courses by showing the nice biocontrol systems that are currently applied in the greenhouse industry and by challenging them to work on new biocontrol solutions.

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*'Biological pest control has been applied very successfully in greenhouse production systems for decades. However, the sector is suffering from new invasions of exotic pest species and an increased pressure of indigenous pests, which both disrupt current biological control strategies. Resilient cropping systems, based on a long-term establishment of multiple species of natural enemies, need to be developed to control the wide range of pests. This requires team building in biocontrol, with natural enemy species playing complementary roles. A better understanding of the underlying mechanisms of the positive effects of natural enemy diversity on pest control can help us to design more effective biological control strategies.'*