

The Influence of Plant Fertilisation Regime on Plant-Aphid-Parasitoid Interactions

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Abstract

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This thesis examines effects of plant fertilisation regime on herbivore and parasitoid performance for two aphids, *Macrosiphum euphorbiae* and *Myzus persicae*, and one parasitoid wasp, *Aphidius ervi*. Herbivore performance was measured as adult fresh weight and intrinsic rate of increase. Parasitoid performance was measured as length of hind tibia, sex ratio, and in a series of choice experiments also parasitoid development time and parasitization rate was measured. Comparisons were made between the performance of *M. euphorbiae* on two different plant species, petunia and sweet pepper, between the performance of the aphids *M. euphorbiae* and *M. persicae* on sweet pepper, and between the performance of *A. ervi* in *M. euphorbiae* and in *M. persicae* on sweet pepper.

The performance of *M. euphorbiae* was better on petunia than on sweet pepper. On petunia a positive effect of plant content of potassium and indications of a positive effect of nitrogen fertilisation were found while on sweet pepper both nitrogen and of potassium had negative influence. On both plant species, however, a negative influence of sulphur was found. The two aphid species reacted differently to fertilisation and plant content of nutrients. For *M. euphorbiae* fresh weight was decreased by fertilisation while for *M. persicae* the influence varied with experiment. For *M. persicae* a high N:K ratio was favourable while for *M. euphorbiae* plant contents of N and K were both negative.

Plant content of sulphur and potassium influenced tibia length of *A. ervi* positively in *M. euphorbiae*. In *M. persicae* plant fertilisation was positive but the composition of the plant fertilisation did not seem important for the parasitoid. Plant fertilisation enhanced parasitization rate in *M. euphorbiae* but not in *M. persicae*. Parasitoid performance was, however, more improved by fertilisation in *M. persicae* than in *M. euphorbiae*. The parasitoid both preferred, and developed faster in, *M. persicae* compared to *M. euphorbiae*.

The results of this study show that it is possible to influence both aphid performance and performance of *A. ervi* with plant fertilisation but the influence varies with both plant and aphid species.

Keywords: *Petunia axillaris hybrida*, *Capsicum annuum*, tritrophic interactions, Plant quality, host quality, insect performance, biological control.

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Contents

Introduction, 7

- Plant nutrients influence on plant, 9
- Plant influence on herbivore, 10
- Herbivore influence on parasitoid, 11
- Plant direct influence on parasitoid, 12
- Plant indirect influence on parasitoid, 13
- Principal aims of the thesis, 14

Studied organisms, 14

- Plants, 14
- Aphids, 15
- Parasitoid, 16

Experiments, results and discussion, 19

- 1) Is aphid performance different on petunia and sweet pepper fertilised with different nutrient regimes? 19
- 2) Do *Macrosiphum euphorbiae* and *Myzus persicae* react differently to the same plant fertilisation on sweet pepper? 20
- 3) Does plant fertilisation influence the performance of *Aphidius ervi* differently in *Macrosiphum euphorbiae* than in *Myzus persicae*? 21
- 4) Is the performance of *Aphidius ervi* influenced when aphids of different nutritional quality or different species are present? 22
- 5) Can plant fertilisation regime influence the success of *Aphidius ervi* when used for biological control of *Macrosiphum euphorbiae* or *Myzus persicae*? 23

References, 24

Acknowledgements, 28

Appendix

Papers I-IV

The present thesis is based on the following papers, which will be referred to by their Roman numerals:

- I. Jansson, J. & Ekbom, B. 2002. The effect of different plant nutrient regimes on the aphid *Macrosiphum euphorbiae* growing on petunia. *Entomologia Experimentalis et Applicata* 104, 109-116.
- II. Jansson, J. & Ekbom, B. The influence of sweet pepper plant nutrient regime on the performance of the aphid *Macrosiphum euphorbiae* and its natural enemy *Aphidius ervi*. (Submitted Manuscript).
- III. Jansson, J. The influence of sweet pepper plant nutrient regime on the performance of the aphid *Myzus persicae* and its natural enemy *Aphidius ervi*. (Manuscript).
- IV. Abugor, I., Jansson, J. & Ekbom, B. Preference and performance of a parasitic wasp on two species of aphids feeding on plants with different fertilisation levels. (Manuscript).

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Introduction

Greenhouse production is a world-wide industry. The greenhouse area is estimated at over 300,000 ha (Gullino et al. 1999). Vegetables are grown in about 65% of the area and ornamentals in 35%. The trend is that there is a shift from growing vegetables to growing ornamentals. Greenhouses are used to extend the growing season and to protect the crop from adverse environmental conditions and from diseases and pests. With modern greenhouse technique it is possible to control both environmental conditions and supply of water and nutrients. Greenhouse crops are often high value-crops that demand a high input of labour and energy, especially during cold and dark periods. In The Netherlands the production value was almost 50 euro/m² in 2000 (Dijkshorn-Dekker, 2002). A high quality of the crop is important, especially for ornamentals where the importance of cosmetic quality means that there is a need to keep plants free from pests. Greenhouse environment is, however, often favourable for pests. International trade with ornamental plants also increases the risk of spreading pests. Invertebrate pests like aphids, thrips, whiteflies, leafminers, and mites are potential disasters in greenhouse crops. Greenhouses may also provide an 'enemy free space' for pests because few naturally occurring enemies enter the greenhouse, especially during the winter season when biological activity may be very low outside the greenhouse.

Greenhouse pests can be suppressed by means such as manipulating environmental conditions, chemical control, and biological control. Biological control means the use of living organisms as pest control agents. Chemical control is easy to apply and relatively inexpensive. In Sweden the cost of chemical control was 0.1-1.3% of the production cost in 2000, depending on crop (Jordbruksverket, 2001). There is, however, an increasing problem with pests that become resistant to the pesticides that are used. The pesticides may also harm non-target organisms and leave chemical residues in the products. Because of this, consumer demand, governmental restrictions, and the grower's concern about their own health there is an increasing interest from the growers to use alternatives to chemical control. Since the start of using biological control in commercial greenhouse production around 1970 large progress has been made. In 1992 over 30 arthropod species were commercially available for biological pest control in greenhouses (Bolckmans, 1999). An estimate of the use of biological control in production in glasshouses made by the IOBC Working Group 'Integrated Control in Protected Crops, Temperate Climate' shows that while biological control is used in a large part of the vegetable greenhouse area it is less widely used in ornamentals. In some areas biological control is used on as much as 80% or more of the greenhouse vegetable area while in ornamentals the percentage in the same area (Canada, Denmark, Finland, Norway, and Sweden), varies between 5-35% (Sting 2003). According to the same source, biological control in Sweden is used on approximately 25% of the ornamental greenhouse area and approximately 85% of the vegetable greenhouse area. That biological control is used in a culture does not exclude that chemical control is also used in the same culture against other pests or to complement the biological control.

In spite of several years of intensive work with biological control the use of natural enemies in commercial greenhouses has not been an unequivocal success and many growers still rely mainly on chemical pesticides to control, for instance, aphids. Biological control is too difficult to use or not efficient enough. One possible reason for the poor results of biological control of aphids in some cases could be the influence of plant quality (such as water and nutrition supply) on the aphids and their natural enemies. If this is the case then it is also a factor that the grower can easily control in a modern greenhouse. Today ornamental growers in Sweden often use one fertiliser that contains all essential plant nutrients and complement with $\text{Ca}(\text{NO}_3)_2$ when more nitrogen is desired.

When using natural enemies to control herbivorous pests it is essential to understand the interactions not only between the herbivores and the enemies but also between the plants and the herbivores and natural enemies that are involved. Manipulation of plant attributes that promote the success of the natural enemies may enhance pest control (Cortesero et al., 2000; Verkerk et al. 1998). Since Price et al. (1980) highlighted the importance of also considering the third trophic level in insect-plant interactions numerous studies of tritrophic interactions have contributed to our knowledge of how plants, herbivores, and parasitoids interact between different trophic levels and what consequences this can have for their respective populations. Tritrophic interactions include various aggressive and defensive interactions both between and within trophic levels, including morphological, behavioural, and physiological relationships (de Moraes et al., 2000). Tritrophic interactions between plants and parasitoids may have evolved in a race between plants and herbivores where there, for instance, has been a competitive advantage for plants that produce more efficient signals when attacked, for parasitoids that utilize these signals, and for herbivores that minimise plant responses to herbivory (de Moraes et al., 2000).

This study is focused on the bottom up interactions and especially effects of plant fertilisation on herbivores and parasitoids (Fig. 1). The influence of a host plant can act directly on the third trophic level for instance by plant volatiles attracting parasitoids, plant structures that hinder parasitoids searching for hosts, or plant structures that can provide parasitoid shelter or food for parasitoids. The influence of a host plant can also act indirectly for instance by influencing the nutritional quality of the parasitoid's host. A parasitoid is also influenced by the host itself, for instance by host species and developmental stage (reviewed by Hågvar & Hofsvang, 1991).

For successful reproduction a parasitoid has to overcome the challenge of habitat identification, host location, host acceptance, host suitability and host regulation. Tritrophic interactions can be important in all these steps. For host location, and host acceptance plant influence on parasitoids is mainly direct while for host acceptance, host suitability, and host regulation plant influence is mainly indirect, through changes in the host (Poppy, 1997).

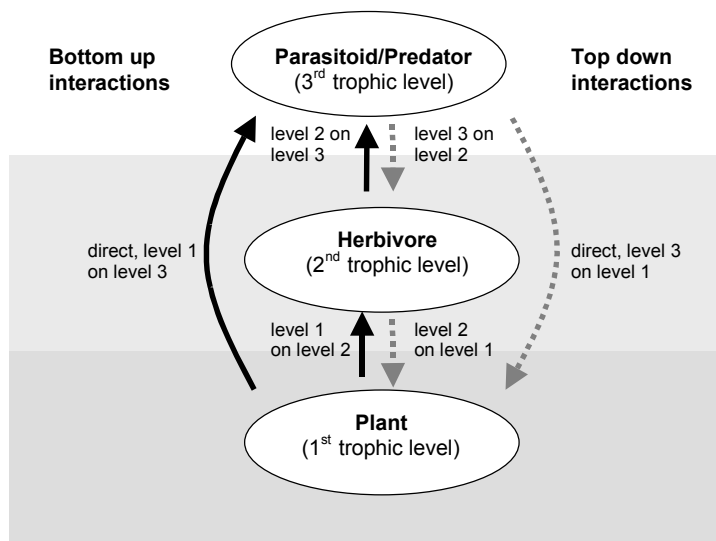


Fig. 1. Conceptual model of interactions between the trophic levels. Solid lines show bottom up interactions, dotted lines show top down interactions.

Plant nutrients influence on plant

Plant growth and the content of nutrients in the plant are influenced by the fertilisation of the plant. Ingestad (1987) suggested that the relative addition rate of each nutrient, rather than nutrient concentration in fertiliser or growth medium is important for plant growth, and that any nutrient in shortage can slow down plant relative growth rate. Some nutrients, e.g. potassium and phosphorous are known to be taken up in excess when available, “luxury consumption” (Mengel & Kirkby, 1982). Excess of nutrients can disturb uptake of other nutrients, in general the increasing supply of one cation species can lead to lower uptake of other cations for instance potassium competes strongly with the uptake of other cations. In anion uptake the antagonism is less common. An increase in nitrogen fertilisation can raise the content of both nitrate and soluble amino acids in the plant, while nitrogen deficiency can lead to hydrolysis of proteins and redistribution of amino acids from older leaves to younger organs. In both cases nitrogen content in the phloem is increased. The phloem is part of the transport system in the plant. In the phloem assimilates are transported from active leaves to growing tissues and break down products are transported from senescing leaves to growing tissues. The phloem content is not only influenced by the plant uptake of nutrients but also by the growth of the plant and shifts between growth and senescence of plant tissues. Potassium is vital for the water balance in the plant and influences the uptake of NO_3^- and the assimilation of CO_2 and potassium deficiency can lead to decreased protein synthesis and accumulation of amino acids (Mengel & Kirkby, 1982), probably due to inadequate energy (ATP) supply.

Phosphorous is essential for energy transfer in the plant and deficiency can affect various processes, such as protein synthesis and active ion uptake and thus lead to retarded plant growth.

The levels of plant secondary metabolites may change under stress. Water stress or potassium deficiency can lead to increased alkaloid content in several plants while deficiency of nitrogen may lead to reduced alkaloid content in plants (Gershenzon, 1984). Alkaloids with high nitrogen content like nicotine seem to be most affected by nitrogen fertilisation.

Plant influence on herbivore

Plants have developed various defences that can limit herbivore damage. Chemical defences that influence the herbivore directly include toxins, repellents, and digestibility reducers while morphological defences include trichomes, spines, surface waxes, and tough foliage (reviewed by Cortesero et al., 2000; de Moraes et al., 2000). Plant toxins, constitutive or induced by plant damage, can kill the herbivores or slow down their growth. Long development time for the herbivores makes them more exposed to predators but less preferred by parasitoids (Williams, 1999). Aphids may avoid ingesting toxic substances by feeding from the phloem. *Myzus persicae* has been shown to avoid nicotine in tobacco plants by feeding on the phloem (Guthrie et al., 1962). Morphological defences have been shown to be negative for herbivores trying to feed on the plants. Glandular hairs on plants can be an obstacle for aphids and other small arthropods. Aphids can get stuck, or if secretion is toxic they can be poisoned (Auclair, 1989).

The quality of the host plant is important for herbivores feeding on it (Koricheva et al., 1998; Waring and Cobb, 1992). Fertilisation and nutrient availability can alter the nutritional quality of the plants and this can influence herbivore growth and reproduction (Larsson, 1989; Waring & Cobb, 1992). 50 years ago Haseman (1950) suggested that plant fertilisation could be used to reduce insect pests by altering the nutrient quality of their food. Most aphids feed directly from the plant phloem and they are considered to be especially influenced by plant conditions such as fertilisation and water stress. Host plant quality has been shown to influence both the size and performance of aphids (Dixon 1998). Nitrogen is one of the plant nutrients that plays an important role for herbivore performance (Mattsson, 1980; Scriber & Slansky, 1981). This is especially true in the case of aphids, because nitrogen content is very low in the phloem. Phloem sap contains 0.004-0.60% nitrogen weight/volume while most plant tissues contain at least 1% nitrogen of dry weight (Mattson, 1980). Nitrogen fertilisation of the plant has, in many cases, been positive for aphids, or sucking insects (reviewed by van Emden 1966 and Waring & Cobb 1992). In a considerable number of the reviewed studies there was, however, no response or the response to nitrogen was negative. One reason for the varying results may be that different aphid species react differently. For instance the nutritional demands are not identical for *Myzus persicae* (Sulzer) (Homoptera: Aphididae) and *Macrosiphum euphorbiae* (Thomas) (Homoptera: Aphididae). Many experiments have shown that *M. persicae* is positively influenced by nitrogen fertilisation (Harrewijn, 1983; Petitt

et al., 1994; Quoilin, 1967). *M. euphorbiae* has been shown to react less negatively to effects of low nitrogen fertilisation than *M. persicae* in experiments on artificial diet and on potato plants (Harrewijn, 1983). Also fertilisation with a high content of sulphur and a low content of phosphorous, (Quoilin, 1967), a high content of magnesium, and a low content of potassium, (Quoilin, 1966), have been shown to be positive for *M. persicae*. Van Emden & Bashford (1969) and Harrewijn (1983) showed that fertilisation with a high N:K ratio was positive for *M. persicae*. There are, however, also contradicting results, for instance Woolridge & Harrison (1968) showed a positive effect of increased potassium fertilisation, on the performance of *M. persicae* on tobacco. High levels of potassium have mostly been shown to influence reproduction negatively, or not at all for aphids and other sucking insects. Waring & Cobb (1992) also concluded that fertilisation with phosphorous most often does not influence sucking insects or influences them positively. The ratios between nutrients have also been shown to influence herbivores (Busch & Phelan, 1999). Van Emden & Bashford (1969) found that a high nitrogen:potassium (N:K) ratio was favourable for *M. persicae* on brussels sprout. Harrewijn (1983) found a positive effect of high N:K ratio in the fertilisation of potatoes on *M. euphorbiae*. Fertilisation may also alter the attractiveness of plants. Rahier (1978) showed that a higher percentage of the plants were infested with alate *M. persicae* in plants with a high N:K ratio than on plants with a lower N:K ratio.

Herbivore influence on parasitoid

The parasitoid may be influenced by the herbivore in all steps from host location to host recognition. Host insect cues such as odours from the host, from host frass, or from honeydew are highly reliable for the parasitoid, but they are not easy to detect in a complicated environment and, especially at longer distances (Vet & Dicke, 1992). *Aphidius ervi* Haliday (Hymenoptera: Aphidiidae), has been shown to also use physical cues to locate its hosts. Losey et al. (1997) found that green morphs of *Acyrtosiphon pisum* (Harris) suffered higher rates of parasitism by *A. ervi* than red morphs of the same species. Battaglia et al. (2000) found that *A. ervi* responded with oviposition attacks to yellow pigments resembling the pigments of *A. pisum* but not to green pigments.

When a host has been found by a parasitoid it can sometimes fight off the parasitoid successfully, by for instance, wriggling or shaking its body, jumping, kicking, falling off the plant or exuding drops of sticky and sometimes toxic liquid from the mouth (Godfray, 1994). Aphids mainly rely on kicking, dropping from the plant and walking away. Dropping from the plant and walking away has been shown to decrease parasitization. The efficacy of defence reactions can vary between aphid species. In a study by Wilbert (1967) *M. persicae* was shown to successfully hinder *Aphelinus flavus* How. from ovipositing in only 58% of oviposition attacks while another species, *Neomyzus circumflexus* (Buckt) hindered oviposition in only 4% of the attacks. Host defence may differ with host age or stage. Gerling et al. (1990) showed that young aphids of *A. pisum* were less able to defend themselves against attacks by the parasitoid *Aphelinus asychis* Walker. If a parasitoid succeeds in ovipositing many hosts can still defend

themselves by a cellular immune reaction called encapsulation. Encapsulation is considered to be the most important factor influencing host suitability for most endoparasitoids. For koinobionts, parasitoids that develop in hosts that continues to feed and grow after parasitization, encapsulation can be especially effective. In the koinobionts the immature parasitoid larvae may be destroyed before it does any permanent damage to the host.

Host species or strain also influences parasitoid performance. For instance some aphids may lack some necessary nutritional or hormonal resource (Hågvar & Hofsvang, 1991) and the ability to encapsulate parasitoid eggs or larvae may vary between aphid species (Wilbert, 1967). For the parasitoid *Aphidius avenae* Haliday the adult wasps from *M. euphorbiae* were larger than the wasps from *M. persicae* (Dunn 1949). It has also been shown that parasitoid preference varies between aphid species. For instance Chow & Mackauer (1991) showed that *A. ervi* preferred *A. pisum* to *Macrosiphum creelii* Davis. *M. euphorbiae* does not seem to be a preferred host for *A. ervi*. Takada and Tada (2000) showed that for a European strain of *A. ervi*, used as a biological control agent in greenhouses, the parasitism rate on *M. euphorbiae* was only 30% while it was over 90% on *A. pisum*.

Parasitoid offspring developing in fast-growing herbivores may have a shorter development time and increased adult body size, fecundity, and survival compared to offspring from a host of poorer quality. It has also been suggested that parasitoids tend to prefer to oviposit in fast-growing herbivores because of the large investment they make in each individual host, which will provide all nutrients needed for the parasitoid's larval development (Barbosa et al. 1982).

Plant direct influence on parasitoid

Studies of tritrophic interactions have shown that parasitoids can react to volatiles released from plants, and use these volatiles to locate host habitats and locate, and oviposit in, suitable hosts. Plant cues are highly detectable to the parasitoid but they are not always reliable, suitable hosts for the parasitoids are not always present on the plants (Vet & Dicke, 1992). Parasitoids that can distinguish attacked plants from plants that are not attacked have an advantage. Induced volatiles emitted from plants damaged by herbivores can attract parasitoids and contribute to a better defence of the plant. This was demonstrated for the plant *Arabidopsis thaliana* (L.), the herbivore *Pieris rapae* L., and the endoparasitoid *Cotesia rubecula* (Marshall) by van Loon et al. (2000). It has also been shown that parasitoids can distinguish between plants damaged by different herbivore species and different developmental stages. *Aphidius ervi* has been shown to use semiochemical cues to locate its host. Powell et al. (1998) and Guerrieri et al. (1999) demonstrated that the parasitoid *A. ervi* can distinguish between odours from plants damaged by *A. pisum* and plants damaged by *Aphis fabae* (Scop.).

Morphological plant structures have been shown to influence parasitoids directly. For instance the presence of leaf hairs can influence the search efficiency of a parasitoid. Stiff hairs on cucumber leaves reduced walking speed for *Encarsia formosa* Gahan and honeydew caught in hairs on the leaves made the parasitoids

use more time for preening and leaving less time for host searching (Hulspas-Jordan & van Lenteren, 1978).

Plants can provide parasitoids with shelter and supplemental food sources. Special structures, leaf domatia that are tufts of hair or pockets on the underside of leaves can provide shelter for natural enemies (Agrawal, 2000). Pollen, nectar, honeydew, and host body fluids can provide food for parasitoids (Leius, 1960). Food supplies natural enemies with energy for locomotion and flight, and to maintain a high longevity and fecundity. Plant food sources can attract parasitoids to the plants (Stapel et al. 1997). Availability and accessibility to food resources strongly affect parasitoids host finding efficacy (reviewed by Lewis et al., 1998).

Plant indirect influence on parasitoid

Nutritional suitability of the host is considered by many authors to be important for the development of parasitoids within certain hosts (Flanders, 1937; Salt, 1938). Nutritional insufficiency in the host can affect development and survival, sex ratio, longevity, fecundity, and the size of the parasitoid wasp (Vinson and Iwantsch, 1980). For koinobiont parasitoids, like *A. ervi*, host quality is determined both by host resources at parasitization and the resources the host acquires during parasitoid development (Mackauer et al., 1997). The quality of an herbivore as a host for a parasitoid is affected by the quality of the herbivore's nutrient intake (Vinson & Barbosa, 1987). Plant fertiliser regime has also been suggested as one way of manipulating plant attributes for improved biological control (Verkerk et al. 1998; Cortesero et al., 2000). In a study by Bentz et al. (1996), parasitization of *Bemisia argentifolii* Bellows & Perring by the parasitoid wasp *E. formosa* was higher on plants treated with calcium nitrate than on unfertilised plants or plants treated with ammonium nitrate. In field and laboratory studies the parasitoid *Diadegma insulare* Cress.'s preferred hosts, diamondback moth (*Plutella xylostella* (L.)), on fertilised plants compared to hosts on unfertilised plants (Fox et al. 1996). In a study by Stadler & Mackauer (1996) the negative effects of unfertilised plants on *A. pisum* were reflected in negative effects on the aphid parasitoid, *Ephedrus californicus* Baker.

The nutritional characteristics of the host's food plant can affect the sex ratio of parasitoids, either by influencing sex allocation or by differentially affecting the survival of sexes. If hosts vary in the amount of resource they contain and if the incremental gain in fitness per host is greater for one sex than the other, then females should allocate that sex to the larger hosts. For instance, it may be better for the female than for the male to grow to a larger size rather than to minimise development time (Charnov, 1979). If the female wasp chooses to lay female eggs in the host with the highest quality this also means that the female offspring might have better resources available for development than male offspring (Mackauer, 1996). In a study by Fox et al. (1990) the proportion of females was higher in the fertilised treatment for the parasitoid *D. insulare* on diamondback moth, *P. xylostella*.

Aphid defence reactions can be influenced by plant quality. In a study by Villagra et al. (2002) the parasitization rate on *A. pisum* parasitized by *A. ervi* on

alfalfa (*Medicago sativa* L.) decreased from 50 to 33 % when the aphids were deprived of food for 48 hours. This was explained by a decrease in dropping and walking away responses of food-deprived aphids.

The plant's chemical defence can also influence parasitoids negatively by influencing the quality of the host. Reed et al. (1992) showed that both aphids and parasitoids were smaller and their development time was longer on resistant grasses compared to susceptible grasses. Toxic allelochemicals from the plants sequestered in the herbivore haemolymph may be detrimental to parasitoids. For example Barbosa et al. (1982) showed that the parasitoid *Apanteles congregatus* (Say) was negatively influenced by nicotine in its host's (tobacco hornworm) diet.

Principal aims of the thesis

In this thesis I have tried to answer some questions about the influence of plant fertilisation on parasitoids used for biological control of aphids. My main questions were:

1. Is herbivore performance influenced by different plant species and their fertilisation?
2. How do different herbivore species react to the same plant fertilisation regimes?
3. Does plant fertilisation influence parasitoid performance differently in different herbivore species?
4. Do interactions between herbivore species and parasitoid influence parasitoid choice when herbivores of different nutritional quality or different species are present?
5. Can plant fertilisation regime influence the success of a parasitoid used for biological control of aphids?

Studied organisms

The organisms I have studied are (Fig. 2) two plants; petunia, *Petunia axillaris hybrida* Villm. Grandiflora Group (Solanaceae) and sweet pepper, *Capsicum annuum* L. (Solanaceae); two aphids, *Macrosiphum euphorbiae* and *Myzus persicae*; and one parasitoid wasp, *Aphidius ervi*.

Plants

Petunia is the largest bedding plant culture in Sweden, next to pansies. In 1999 almost 10,000,000 plants were produced according to official statistics

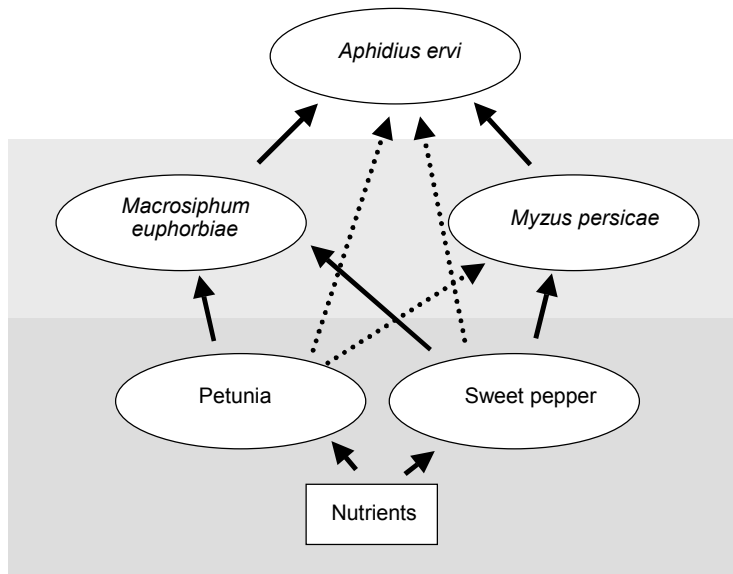


Fig. 2. Studied organisms and bottom up interactions between the trophic levels. Solid lines show interactions studied in the experiments.

(Trädgårdsräkningen 2000, 2000). The petunia plants used in the experiments were seed propagated varieties ‘Dreams Salmon’ and ‘Ultra Salmon’. Petunia leaves are covered with trichomes with sticky exudates that can be toxic to insects (Thurston, 1970) and protect them from herbivore damage. Aphids have not been a serious pest problem in petunia culture when plants were grown from seeds but since new varieties, propagated by cuttings, have become common in greenhouse production the risk for spreading aphids in petunia crops has also increased. An increased use of biological control of other pests has increased the need for compatible methods against aphids (Rabasse & van Steenis, 1999).

Sweet pepper was chosen for the experiments because it belongs to the same family as petunia (Solanaceae), both *M. euphorbiae* and *M. persicae* are recorded as pests on sweet pepper, the plants have no hairs on their leaves, and the plant is easy and quick to propagate, (Blackman and Eastop, 2000). Pepper is an important crop world-wide and grown on about 1,200,000 ha (Dik et al., 1999). Most of the peppers are grown outdoors, but in Spain for instance 9000 ha is under protected cultivation (Dik et al., 1999).

Aphids

Aphids are among the most important pests in greenhouse crops (Brødsgaard & Albajes, 1999), especially those belonging to the family Aphididae. The aphids *M. euphorbiae* and *M. persicae* are both polyphagous and on annual greenhouse

crops they reproduce only by parthenogenesis (Ramakers, 1989). Aphids reproduce very quickly, their intrinsic rate of increase normally being 0.2-0.3 female per female per day (Rabasse & van Steenis, 1999), and this makes them very difficult to control, especially in greenhouse production where the environment is favourable and natural enemies are excluded. Aphids have also developed resistance against many insecticides, for instance the specific aphicide pirimicarb (Dik et al. 1999). The recent introduction of some easy-to-use systemic aphidicides such as imidacloprid has, however, temporarily solved this problem.

Macrosiphum euphorbiae has almost world-wide distribution (Blackman and Eastop, 2000). The adult apterae are large, 1.7-3.6 mm (Blackman and Eastop, 2000), and mobile. They are more active than *M. persicae* and when disturbed they fall readily to the ground (Dunn, 1949). The adult apterae are usually some shade of green and rather shiny which makes them easy to distinguish from the nymphs that are usually covered by a thin wax layer. Primary hosts are *Rosa spp.* L.

Myzus persicae is extremely polyphagous and also has a world-wide distribution. The adult apterae are somewhat smaller than *M. euphorbiae*, 1.2-2.1 mm (Blackman and Eastop, 2000) and vary in colour from whitish green to mid green, red or almost black. The aphids in our experiments were green as young nymphs and mid green-red as adult apterae. Primary hosts are *Prunus persicae* L., sometimes *P. nigra* or *P. tenella* Batsch, and possibly *P. serotina* Ehrh. and peach-almond hybrids. *Myzus persicae* is the most harmful aphid in sweet pepper production (Schepers, 1989).

Parasitoid

Aphidius ervi is a parasitoid wasp that has been used for biological control of aphids in greenhouses since 1996 (Bolckmans, 1999), mainly against *M. euphorbiae* and *Aulacorthum solani* (Kaltenbach). The adult wasp is approximately 4.5 mm long (Dunn, 1949) slender and dark (Stary, 1974)

The female parasitoid lays eggs in several species of aphids, for instance *Acyrtosiphon pisum* (Harris), *Sitobion avenae* (Fabricius), *M. persicae*, *M. euphorbiae* and *Rhopalosiphum padi* (L.) (Stary, 1974). When the female has located a potential host she attacks the aphid with the head facing the host and extending the abdomen forward between her legs and under her thorax during oviposition. *Aphidius ervi* use less than 0.5 seconds to oviposit (Völkl & Mackauer, 2000) and avoid direct body contact with the host. The parasitoid lays a minute egg (0.1 mm) in the aphids body cavity (Rabasse & van Steenis, 1999) (Fig. 3). The larva hatches after a few days and feeds from the haemolymph. First the larva feeds osmotically then in stages 2-3 it feeds orally (Stary, 1988). The fourth-instar larva consumes the remaining tissues and the host dies. The parasitoid cuts a slit in the underside of the aphid cuticle and spins its cocoon inside attaching the formed “mummy” to the leaf by the silk appearing in the slit (Rabasse & van Steenis, 1999). The wasp pupates inside the mummy and the adult wasp emerges, cutting a circular lid in the top of the mummy a few days later. The

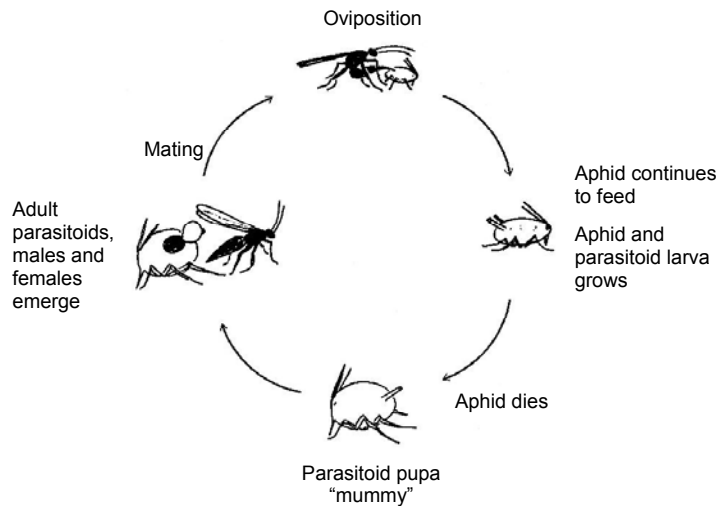


Fig. 3. Life cycle of *A. ervi*.

parasitoid may lay an egg in a host that has already been parasitized by a member of the same species, superparasitism, but only one parasitoid can develop in each aphid. Development time from oviposition to emergence of adult parasitoid is 20 days in *M. persicae* on sweet pepper at 21 °C (Hofsvang & Hågvar, 1975). In *A. pisum* on alfalfa, *Medicago sativa* L., development time from oviposition to emergence of adult parasitoid at 19.7 °C is 14.4 days (Campbell & Mackauer, 1975).

Fertilised eggs result in females and unfertilised eggs in males. A fertilised female can control the sex of each individual progeny by fertilising or not fertilising the egg when ovipositing (Quicke, 1997). Charnov et al. (1981) suggests that females should allocate fertilised eggs (daughters) to high value hosts and unfertilised eggs (sons) to low value hosts. A female-biased sex ratio is efficient in parasitoid rearing because of a higher intrinsic rate of increase in a population with many females (Hall, 1993). It is important, however, that a sufficient number of males are present to insure efficient mating and that the ability of the parasitoid to adapt to changing environmental conditions is not lost (Hall, 1993). The adult females mate only once while males can mate several times (Hågvar & Hofsvang, 1991). In inundative release programmes in augmentative biological control where large numbers of parasitoids are released several times in the growing season and establishment of a wasp population is not expected it is efficient with a strong female biased sex ratio since females are more efficient “pest killers” (Hall, 1993). Sex ratio in wasps used for biological control should be $\geq 45\%$ females to be considered good quality (van Lenteren, 1993).

Aphidius ervi has a great potential for successful control of aphids with its short development time, high fecundity and high dispersal capacity (Rabasse & van Steenis, 1999). The effects of parasitoids on aphid populations can be several (Stary 1988): 1) Aphids that are successfully parasitized die, 2) repeated oviposition stings may cause lethal injury to the aphid, and 3) the aphids can be disturbed and run or fall off the plant (both males and females can disturb them) and may not be able to get up again because of predators or low soil temperature. Repeated parasitoid attacks on an aphid colony causes a disturbance that can result in considerable mortality that sometimes is more important than the parasitization itself (Ramakers, 1989). Host feeding by adults is common in some parasitoid species and may contribute considerably to aphid mortality. Mackauer & Kambhampati (1988) have shown, however, that adult *A. ervi* do not host feed but obtain nutrients chiefly from plant nectar and aphid honeydew.

In the experiments we measured parasitoid size as hind tibia length. To establish the relationship between tibia length and parasitoid weight we weighed and measured tibia length on 260 newly emerged parasitoids from Koppert B.V., The Netherlands. Adult parasitoids were killed by freezing within 17 hours after emergence. Their sex was determined and then the parasitoids were dried at 70 °C for 3.5 days. Dry weight was measured on a Cahn balance to the nearest 0.01 mg. Tibia length was then measured as in the experiments, to the nearest 0.01mm. We found a clear relation between tibia length (TL) and dry weight (DW) for both female and male parasitoids (Fig. 3). Female tibia length: $TL = 0.56 + 1.33 * DW$, $r^2 = 0.74$, $F = 339.07$, $df = 1,119$, $P < 0.0001$. Male tibia length: $TL = 0.48 + 1.28 * DW$, $r^2 = 0.72$, $F = 356.24$, $df = 1,141$, $P < 0.0001$. Tibia lengths in the experiments were within the same range as tibia lengths in Fig. 4.

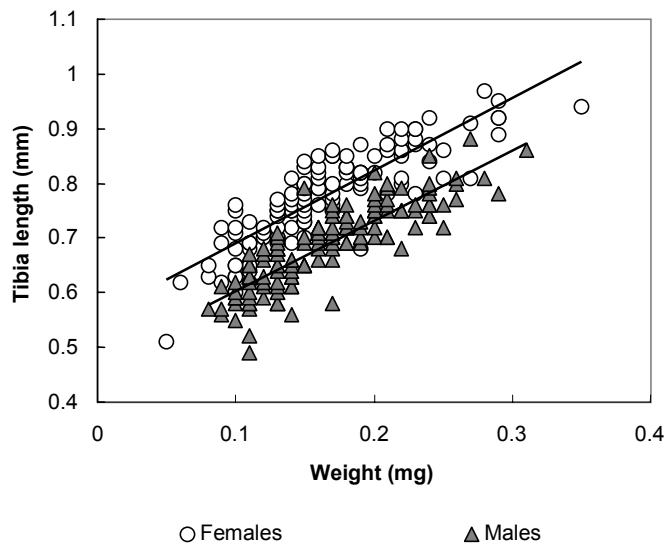


Fig. 4. Relation between wasp tibia length and dry weight.

Experiments, results and discussion

1) Is aphid performance different on petunia and sweet pepper fertilised with different nutrient regimes?

In a series of experiments with *M. euphorbiae* on petunia plants (Paper I) and another series of experiments with *M. euphorbiae* on sweet pepper plants (Paper II) aphid performance in relation to plant fertilisation and plant content of nutrients was measured. The plants were treated with different fertilisation regimes; one treatment with no fertilisation added, one with a high N:K ratio and one with a low N:K ratio. In one of the experiments on sweet pepper (Paper II) we also used a high phosphorous, a low nitrogen, only potassium and sulphur, and only nitrogen and calcium treatments. Aphid performance was measured as development time, number of offspring, and adult fresh weight. Development time and number of offspring were used to calculate the intrinsic rate of increase of the aphid.

On petunia phosphorous had a positive effect on several parameters of performance for *M. euphorbiae* (Paper I). Plant content of phosphorous was positively related to number of offspring of apterous aphids, longevity of alatae, and fresh weight of adult apterous aphids. Short development times were associated both with high phosphorous and high potassium content in leaves but due to correlation between the nutrients it was not possible to know the relative importance of these nutrients. We found indications of a positive effect of nitrogen fertilisation on aphid performance as intrinsic rate of increase was positively influenced by nitrogen. We did not find any relation between N:K ratios in the plants and performance of *M. euphorbiae* on petunia except for a weak association with shorter pre reproductive time for the alatae aphids we placed on the plants. Sulphur was found to be negatively associated with both intrinsic rate of increase and adult fresh weight.

On sweet pepper the performance of *M. euphorbiae* was negatively influenced by plant contents of sulphur, nitrogen, and potassium (Paper II). Aphid weight and rate of increase decreased with increasing levels of sulphur in the plant and aphid weight was also negatively correlated to plant content of nitrogen and potassium.

It is clear from these results that the response of *M. euphorbiae* to fertilisation was different between the two plant species. Aphid fresh weight was increased by fertilisation on petunia while it was decreased on sweet pepper. On petunia a positive effect of plant content of potassium was found and indications of a positive effect of nitrogen fertilisation. On sweet pepper a negative influence both of nitrogen and of potassium was found. On both plant species, however, a negative influence of sulphur was found. Possible explanations of the differences found in aphid responses can be 1) if plant content of secondary compounds that are toxic to aphids was influenced in different directions in the two plant species, 2) if plant content of amino acids essential for the aphids was influenced in different directions in the two plant species, 3) If there is an optimal level of plant

content nitrogen and potassium and that plant content was above the optimum in the experiments on sweet pepper and below it in the experiments with petunia.

In general the performance of *M. euphorbiae* was better on petunia than on sweet pepper. The intrinsic rate of increase was significantly higher on petunia ($F=14.46$, $df=1,15$, $P=0.003$) than on sweet pepper when compared in an ANOVA using treatment means and with plant and treatment as factors, and there was no interaction between plant and treatment. On petunia the intrinsic rate of increase was 0.21 ± 0.01 SE and on sweet pepper it was 0.15 ± 0.01 SE. The experiments were, however, performed at different times and under different conditions so it is not possible to know to what extent the plant influenced these differences and to what extent it was caused by different climatic conditions. Culliney & Pimentel (1985) found slightly higher intrinsic rate of increase for *M. persicae* on Collards (*Brassica oleracea*) at 25 °C it was 0.348, El Din (1976) found even higher values on leaf discs of brussels sprouts, 1.8 at 20 °C and 1.8 at 25 °C.

We repeated the experiments with *M. persicae* on petunia. Petunia was, however, not a good host plant for the strain of *M. persicae* that we used in our experiments. In one experiment (unpublished) we placed 20 newly moulted alatae *M. persicae* per treatment on petunia plants. The treatment of the plants was the same as in Paper I, experiments 1998 and 1999. In treatments 0 and 2 all alatae and nymphs were dead within 10 days. In treatment 1 all alatae except 4 were dead within 10 days. 35 nymphs were born during these 10 days and 3 of the nymphs lived until they became adult and started to reproduce.

2) Do *Macrosiphum euphorbiae* and *Myzus persicae* react differently to the same plant fertilisation on sweet pepper?

In two series of experiments on sweet pepper plants, one with *M. euphorbiae* (Paper II) and one with *M. persicae* (Paper III) aphid performance in relation to plant fertilisation and plant content of nutrients was measured. The plants were treated with different fertilisation regimes as described above. Fresh weight of adult aphids was measured and intrinsic rate of increase was calculated from development time and number of offspring.

The adult weight of *M. persicae* was positively correlated with plant N:K ratio (Paper III). Adult weight and intrinsic rate of increase of *M. euphorbiae* decreased with increasing levels of sulphur in the plant and aphid weight was also negatively correlated to plant content of nitrogen and potassium as described above (Paper II).

Intrinsic rate of increase was generally higher for *M. persicae* than for *M. euphorbiae*. For *M. persicae* it was 0.30 ± 0.01 SE and for *M. euphorbiae* it was 0.18 ± 0.01 SE. One reason for this difference was that *M. persicae* had a shorter development time than *M. euphorbiae*. When comparing the treatment means from all experiments on sweet pepper, except treatments 3-6 in July in an ANOVA with aphid and treatment as factors the intrinsic rate of increase was significantly higher for *M. persicae* than for *M. euphorbiae* ($F=39.91$, $df=1,21$, $P<0.001$). Climatic conditions may have contributed to this difference but the intrinsic rate of increase

was also approximately twice as high for *M. persicae* as for *M. euphorbiae* in an experiment performed at the same time and in the same greenhouse compartment (Paper II experiment B and Paper III experiment I).

It is evident from the results of these experiments that the two aphid species react differently to plant fertilisation and plant content of nutrients. Fresh weight of *M. euphorbiae* on sweet pepper was decreased by fertilisation while fresh weight of *M. persicae* was influenced in different directions by fertilisation in different experiments. For *M. persicae* a high N:K ratio created favourable conditions for the aphid while for *M. euphorbiae* both plant content of N and of K were negative for aphid performance. This difference in results between the two aphids supports the idea that the nutritional demands are not identical for *M. persicae* and *M. euphorbiae* (Harrewijn, 1989), and that *M. persicae* reacts more negatively to low N content in the fertilisation than the aphid *M. euphorbiae* (Harrewijn, 1983).

3) Does plant fertilisation influence the performance of *Aphidius ervi* differently in *Macrosiphum euphorbiae* than in *Myzus persicae*?

The performance of the parasitoid *A. ervi* in relation to plant fertilisation and plant content of nutrients was measured in the same two series of experiments on sweet peppers as described above (Paper II and Paper III). Wasp performance was measured as adult hind tibia length and sex ratio.

For parasitoids from *M. euphorbiae* (Paper II) the tibia length was positively correlated to plant content of sulphur and potassium. For parasitoids from *M. persicae* (Paper III) the tibia length was positively influenced by fertilisation, but no significant correlation with plant nutrient content could be found.

The results of the experiments show that the composition of the plant fertilisation is important for the performance of *A. ervi* in *M. euphorbiae*. On sweet pepper the plant content of sulphur and of potassium was positive for tibia length. For the performance of *A. ervi* in *M. persicae*, however, plant fertilisation is positive but the composition of the plant fertilisation does not seem to be as important as for parasitoids in *M. euphorbiae*. Good host quality has been shown to be associated with two parasitism specific proteins for *A. ervi* (Pennacchio et al., 1999). Plant nutrient content and plant species might play a role in synthesis of these proteins. The results also support the idea that the quality of the host, rather than the size, is important for adult size of *A. ervi*, something that has also been shown for the pea aphid-*A. ervi* system (Sequeira and Mackauer 1992).

We also carried out an experiment where we let *A. ervi* parasitize *M. euphorbiae* on petunia plants. In this experiment we found a very low parasitization rate on petunia plants. When watching the parasitoids on petunia leaves in the laboratory they spent a lot of time preening. One possible explanation of the low parasitization on petunia might be that the parasitoids were disturbed by the glandular hairs on the leaves.

4) Is the performance of *Aphidius ervi* influenced when aphids of different nutritional quality or different species are present?

The performance of *A. ervi* in relation to plant fertilisation was measured in three choice experiments, one with *M. euphorbiae* and two with *M. persicae*, one with 10 pairs of parasitoids and one with 3 pairs (Paper IV). In another choice experiment the performance of *A. ervi* in relation to aphid species was measured (Paper IV). In the experiments wasp performance was measured as percent parasitization, adult hind tibia length, and sex ratio. In these choice experiments the nutrient composition was not the same as in the experiments in Papers I, II, and III.

For *M. euphorbiae* the proportion of parasitized aphids and the proportion of female wasps was higher on fertilised than on unfertilised sweet pepper plants. Development time of male parasitoids was longer on fertilised plants. For *M. persicae* no difference in the proportion of parasitization could be found between fertilised and unfertilised plants but in the experiment with fewer parasitoids the proportion of females was higher on the fertilised plants. Tibia length was positively influenced by fertilisation for male parasitoids from *M. persicae*. Development time of the parasitoids was longer on fertilised plants for both males and females.

The percent of parasitization was higher for *M. persicae* than for *M. euphorbiae* when *A. ervi* was given a choice between these two aphid species. Development time was also shorter in *M. persicae* than in *M. euphorbiae*.

The parasitoid seems to prefer *M. euphorbiae* on fertilised plants although offspring sizes were not significantly larger on fertilised plants compared to unfertilised. For *M. persicae* the result was different, although fertilisation did not increase parasitization rate for *M. persicae*, wasp performance was better on hosts from fertilised plants. Two factors may both have contributed to the higher parasitism of *M. euphorbiae* on the fertilised plants: 1) the parasitoid's choice, and 2) a higher survival of parasitoid larvae in aphids on fertilised plants. If the female parasitoid can assess the quality of its host we would assume that the parasitoid would prefer to oviposit in the hosts that will be best for the development of parasitoid offspring. In this experiment this does not seem to be the case. In another study (Paper II) plant fertilisation could, however, be positive for *A. ervi* on *M. euphorbiae*. The proportion of female parasitoids was higher in the fertilised than in the unfertilised plants in the choice experiment with *M. euphorbiae* and in one of the choice experiments with *M. persicae*. The higher proportion of females in the fertilised treatment is similar to results with diamondback moth and its parasitoid *D. insulare* (Fox et al., 1990).

Parasitoid development time was longer on fertilised plants than on unfertilised plants in some cases. This might seem contrary to expectations that better nourished hosts would allow the parasitoids to develop more quickly. However, Kouamé & Mackauer (1991) found that a braconid parasitoid developed faster on starved aphids. Either resources are scarce or cellular defences weakened in poor-condition hosts, which results in faster development than in good-condition hosts (Godfray 1994).

The positive effect of plant fertilisation on parasitization rate that was found in *M. euphorbiae* was not found in *M. persicae*. At the same time parasitoid performance was more improved by fertilisation for parasitoids developing in *M. persicae* compared to in *M. euphorbiae*. It was also clear that the parasitoid both preferred, and developed faster in, *M. persicae* compared to in *M. euphorbiae*. Although development time of males was approximately 1 day shorter for *A. ervi* in *M. persicae* than in *M. euphorbiae* no difference was found in size. This result indicates that relative growth rate of the parasitoid larvae might be higher in *M. persicae* than in *M. euphorbiae*. The better host quality of *M. persicae* may depend on a better quality of the nutrient content in that aphid species, a larger supply of nutrients or both. The higher intrinsic rate of increase, or faster development of the nymphs might be beneficial for the parasitoid.

5) Can plant fertilisation regime influence the success of *Aphidius ervi* when used for biological control of *Macrosiphum euphorbiae* or *Myzus persicae*?

It is clear from this study that the influence of specific plant nutrients on aphid performance varies with both aphid species and plant species. In greenhouse production of ornamentals where many different plant species are grown in the same greenhouse or greenhouse compartment this can be a practical problem. Plant fertilisation can also only be used to reduce insect pests if the influence on plant performance is not negative for product quality or yield. It may not be feasible to fertilise all plant species with different fertilisation regimes and some compromises have to be made. The results do, however, indicate that fertilising sweet pepper plants with a high level of potassium might be unfavourable for both *M. euphorbiae* and *M. persicae*.

It is also clear from this study that the influence of specific plant nutrients on parasitoid performance varies with aphid species. On sweet pepper tibia length was positively correlated to plant content of sulphur and potassium for parasitoids in *M. euphorbiae* but no for parasitoids in *M. persicae*. Fertilisation was positive for the proportion of parasitized *M. euphorbiae* while the proportion of parasitized *M. persicae* was not influence by fertilisation. It is not uncommon that more than one aphid species is present in the same greenhouse compartment. If the parasitoid reacts differently to fertilisation for different aphid species this may cause a problem when trying to choose the best fertilisation regime.

Aphidius ervi preferred, and developed faster in, *M. persicae* compared to *M. euphorbiae*. This means that if both *M. euphorbiae* and *M. persicae* are present on the plants it might be difficult to make biological control of *M. euphorbiae* work with *A. ervi* alone.

Even if plant fertilisation influences the performance of *A. ervi* the influence of climatic conditions seems to be larger. At 14.8 °C development time for *A. ervi* was 23.0 days, at 19.7 °C it was 14.4 days, and at 26.1 °C it was 10.8 days (Campbell & Mackauer, 1975). In this same interval the effects on the host, *A. pisum* were, however, also positive and the development times were 12.1, 7.6,

respectively 5.4 and this partially outweighs the effects of shorter development time of the parasitoid. In our experiments we have shown that the effects of fertilisation on aphid and wasp performance may act in different directions and this means that they strengthen each other. Even if the effect may be small it should not be neglected as a tool to enhance biological control. Fertilisation regime alone may, however, not be so important for the effect of biological control of aphids but should be regarded as one of several tools to enhance the effect of parasitoids.

The results of this study show that it is possible to influence both aphid performance and performance of *A. ervi* with plant fertilisation. This supports the theories that plant fertilisation can be used to reduce insect pests by altering the nutrient quality of their food (Haseman, 1950) and that manipulation of the plant may promote the success of the natural enemies and enhance the pest control (Cortesero et al., 2000).

References:

- Agrawal, A.A. 2000. Mechanisms, ecological consequences and agricultural implications of tri-trophic interactions. *Current Opinion in Plant Biology*, 329-335.
- Auclair, J.L. 1989. Host Plant Resistance, in Greenhouses, In: *World Crop Pests, 2C, Aphids Their Biology, Natural Enemies and Control*, eds. Minks, A.K. & Harrewijn, P., Elsevier, Amsterdam, The Netherlands, 225-265 pp.
- Barbosa P., Sauders, J.A. & Waldvogel, M. 1982. Plant mediated variation in herbivore suitability and parasitoid fitness. In: *Proceedings of the 5th Symposium on Insect-plant Relationships*, eds. Visser, J.H. & Minks A.K., Pudoc, Wageningen, The Netherlands, 63-71 pp.
- Battaglia, D., Poppy, G., Powell, W., Romano, A., Tranfaglia, A. & Pennacchio, F. 2000. Physical and chemical cues influencing the oviposition behaviour of *Aphidius ervi*. *Entomologia Experimentalis et Applicata* 94, 219-227.
- Bentz J-A., Reeves J., Barbosa, P., & Francis, B. 1996. The effect of nitrogen fertilizer applied to *Euphorbia pulcherrima* on the parasitization of *Bemisia argentifolii* by the parasitoid *Encarsia formosa*. *Entomologia Experimentalis et Applicata* 78, 105-110.
- Blackman, R.L. & Eastop, V.F. 2000. *Aphids on the World's Crops: An Identification and Information Guide*. John Wiley and Sons Ltd, Chichester, UK.
- Bolckmans, K.J.F. 1999. Commercial Aspects of Biological Pest Control in Greenhouses. In: *Integrated Pest and Disease Management in Greenhouse Crops*, eds. Albajes, R., Gullino, M.L., van Lenteren, J.C. and Elad, Y., Kluwer Academic Publishers, Dordrecht, The Netherlands, 310-318 pp.
- Brødsgaard, H.F. & Albajes, R. 1999. Insect and mite pests. In: *Integrated Pest and Disease Management in Greenhouse Crops*, eds. Albajes, R., Gullino, M.L., van Lenteren, J.C. and Elad, Y., Kluwer Academic Publishers, Dordrecht, The Netherlands, 48-60 pp.
- Busch, J.W., Phelan, P.L. 1999. Mixture models of soybean growth and herbivore performance in response to nitrogen-sulphur-phosphorus nutrient interactions. *Ecological Entomology* 24, 132-145.
- Campbell, A. & Mackauer, M. 1975. Thermal constants for development of the pea aphid (Homoptera: Aphididae) and some of its parasitoids. *The Canadian Entomologist* 107, 419-423.
- Charnov, E.L. 1979. The genetical evolution of patterns of sexuality: Darwinian fitness. *The American Naturalist* 113, 465-480.
- Charnov, E.L., Los-den Hartogh, R.L., Jones, W.T. & van den Assem, J. 1981. Sex ratio evolution in a variable environment. *Nature* 289, 27-33.

- Chow, A. & Mackauer, M. 1991. Patterns of host selection by four species of aphidiid (Hymenoptera) parasitoids: influence of host switching. *Ecological Entomology* 16, 403-410.
- Cortesero, A.M., Staple, J.O., and Lewis, W.J. 2000. Understanding and Manipulating Plant Attributes to Enhance Biological Control. *Biological Control* 17, 35-49.
- Culliney, T.W. & Pimentel, D. 1985. The intrinsic rate of natural increase of the green peach aphid, *Myzus persicae* (Sulzer) (Homoptera: Aphididae), on collards (*Brassica oleracea* L.). *The Canadian Entomologist* 117, 1147-1149.
- Dijkshoorn-Dekker, M.W.C. 2002. *Crop quality control system: a tool to control the visual quality of pot plants*. Doctoral thesis, Wageningen Universiteit, Wageningen, The Netherlands.
- Dik, A.J., Ceglarska, E. & Ilovai, Z. 1999. Sweet Peppers. In: *Integrated Pest and Disease Management in Greenhouse Crops*, eds. Albajes, R., Gullino, M.L., van Lenteren, J.C. and Elad, Y., Kluwer Academic Publishers, Dordrecht, The Netherlands, 473-485 pp.
- Dixon, A.F.G. 1998. *Aphid Ecology An Optimization approach*. 2nd edition. Chapman & Hall, London.
- Dunn, J.A. 1949. The parasites and predators of potato aphids. *Bulletin of Entomological Research* 40, 97-122.
- El Din, N.S. 1976. Effects of temperature on the aphid, *Myzus persicae* (Sulz.), with special reference to critically low and high temperature. *Zeitschrift für Angewandte Entomologie* 80, 7-14.
- van Emden, H.F., 1966. Studies on the relations of insect and host plant. III. A comparison of the reproduction of *Brevicoryne brassicae* and *Myzus persicae*: (Hemiptera: Aphididae) on brussels sprout plants supplied with different rates of nitrogen and potassium. *Entomologia Experimentalis et Applicata* 9, 444-460.
- van Emden, H.F. & Bashford, M.A. 1969. A comparison of the reproduction of *Brevicoryne brassicae* in relation to soluble nitrogen concentration and leaf age (leaf position) in the Brussels sprout plant. *Entomologia Experimentalis et Applicata* 12, 351-364.
- Flanders, S.E. 1937. Starvation of developing parasites as an explanation of immunity. *Journal of Economic Entomology* 30, 970-71.
- Fox, L.R., Letourneau, D.K., Eisenbach, J. & Van Nouhuys, S. 1990. Parasitism rates and sex ratios of a parasitoid wasp: effects of herbivore and plant quality. *Oecologia* 83, 414-419.
- Fox, L.R., Kester, K.M. & Eisenbach, J. 1996. Direct and indirect responses of parasitoids to plants: sex ratio, plant quality and herbivore diet breadth. *Entomologia Experimentalis et Applicata* 80, 289-292.
- Gerling, D., Roitberg, B.D. & Mackauer, M. 1990. Instar-specific defence of the pea aphid, *Acyrtosiphon pisum*: Influence on oviposition success of the parasite *Aphelinus asychis* (Hymenoptera: Aphelinidae). *Journal of Insect Behavior* 3, 501-514.
- Gershenson, J. 1984. Changes in the levels of plant secondary metabolites under water and nutrient stress. In: *Recent advances in phytochemistry Vol. 18, Phytochemical adaptations to stress*, eds. Timmermann, B.N., Steelink, C. & Loewus, F., Plenum Press, New York, 273-321.
- Godfray, H.C.J. 1994. *Parasitoids: Behavioural and Evolutionary Ecology*. Princeton, New Jersey, USA.
- Guerrieri, E., Poppy, G.M., Powell, W., Tremblay, E. & Pennacchio, F. 1999. Induction and systemic release of herbivore-induced plant volatiles mediating in-flight orientation of *A. ervi*. *Journal of Chemical Ecology* 25, 1247-1261.
- Gullino, M.L., Albajes, R. & van Lenteren, J. 1999. Setting the stage: characteristics of protected cultivation and tools for sustainable crop protection. In: *Integrated Pest and Disease Management in Greenhouse Crops*, eds. Albajes, R., Gullino, M.L., van Lenteren, J.C. and Elad, Y., Kluwer Academic Publishers, Dordrecht, The Netherlands, 1-15 pp.
- Guthrie, F.E., Campbell, W.V. & Baron, R.L. 1962. Feeding sites of the green peach aphid as a possible explanation of the adaption to tobacco. *Annals of the Entomological Society of America* 55, 42-46.

- Hall, R.W. 1993. Alteration of sex ratios of parasitoids for use in biological control. In: *Evolution and diversity of sex ratio in insects and mites*, eds. Wrensch, D.L. & Ebbert, M.A., Chapman & Hall, New York, USA, 543-547 pp.
- Harrewijn, P. 1983. The effect of cultural measures on behaviour and population development of potato aphids and transmission of viruses. *Mededelingen van de Rijksfakulteit Landbouwwetenschappen te Gent* 48, 791-799.
- Harrewijn, P. 1989. Integrated Control of Potato Aphids. In: *World Crop Pests, Aphids Their Biology, Natural Enemies and Control*, 2C, eds. Minks, A.K. & Harrewijn, P., Elsevier, Amsterdam, The Netherlands, 279-284 pp.
- Haseman, L. 1950. Controlling insect pests through their nutritional requirements. *Journal of economic entomology* 43, 399-401.
- Höfsvang, T. & Hågvar, E.B. 1975. Duration of development and longevity in *Aphidius ervi* and *Aphidius platensis* (Hym.: Aphidiidae), two parasites of *Myzus persicae* (Hom.: Aphididae). *Entomophaga* 20, 11-22.
- Hulspas-Jordan, P.M. and van Lenteren, J.C. 1978. The relationship between host-plant leaf structure and parasitization efficiency of the parasitic wasp *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae). *Mededelingen van de Rijksfakulteit Landbouwwetenschappen te Gent* 43, 431-440.
- Hågvar, E.B. & Hofsvang, T. 1991. Aphid parasitoids (Hymenoptera, Aphidiidae): biology, host selection and use in biological control. *Biocontrol News and Information* 12, 13-41.
- Ingestad, T. 1987. New concepts on soil fertility and plant nutrition as illustrated by research on forest trees and stands. *Geoderma* 40, 237-252.
- Jordbruksverket, 2001. Trädgårdsnäringens växtskyddsförhållanden. *Jordbruksverket, Rapport 2001:7A*.
- Kouamé, K.L. & Mackauer, M. 1991. Influence of aphid size, age and behaviour on host choice by the parasitoid wasp *Ephedrus californicus*: A test of host-size models. *Oecologia* 88, 197-203.
- Koricheva, J., Larsson, S., & Haukioja, E. 1998. Insect performance on experimentally stressed woody plants: A meta analysis. *Annual Review of Entomology* 43, 195-216.
- Larsson, S. 1989. Stressful times for the plant stress-insect performance hypothesis. *Oikos* 56, 277-283.
- Leius, K. 1960. Attractiveness of different foods and flowers to the adults of some hymenopterous parasites. *The Canadian Entomologist* 92, 369-376.
- van Lenteren, 1993. Quality control for natural enemies used in greenhouses. *IOBC WPRS Bulletin* 16, pp.89-92.
- Lewis, W.J., Staple, O.J., Cortesero, A.M. & Takasu, K. 1998. Understanding how parasitoids balance food and host needs: importance to biological control. *Biological Control* 11, 175-183.
- van Loon, J.J.A., de Boer, J.G., Dicke, M. 2000. Parasitoid-plant mutualism: parasitoid attack of herbivore increases plant reproduction. *Entomologia Experimentalis et Applicata* 97, 219-227.
- Losey, J.E., Ives, A.R., Harmon, H., Ballantyne, F. & Brown, C. 1997. A polymorphism maintained by opposite patterns of parasitism and predation. *Nature* 388, 269-272.
- Mackauer, M. 1996. Sexual size dimorphism in solitary parasitoid wasps: influence of host quality. *Oikos* 76, 265-272.
- Mackauer, M. & Kambhampati, S. 1988. Sampling and rearing of aphid parasites. In: *World Crop Pests, Aphids Their Biology, Natural Enemies and Control*, 2B, eds. Minks, A.K. & Harrewijn, P., Elsevier, Amsterdam, The Netherlands, 205-216 pp.
- Mackauer, M., Sequeira, R., Otto, M., 1997. Growth and Development in Parasitoid Wasps: Adaption to Variable Host Resources. In: *Ecological Studies, Vol.130. Vertical Food Web Interactions: Evolutionary Patterns and Driving Forces*, eds. Dettner, K., Bauer, G., Völkl, W., Springer-Verlag, Berlin, 191-203 pp.
- Mattsson, W.J. 1980. Herbivory in relation to plant nitrogen content. *Annual review of ecology and Systematics* 11, 119.
- Mengel, K. & Kirkby, E.A. 1982. *Principles of plant nutrition*. 3rd edition. International potash institute, Bern, Switzerland.

- Michaud, J.P. 1996. The oviposition behaviour of *Aphidius ervi* and *Monoctonus paulensis* (Hymenoptera: Aphidiidae) encountering different host species (Homoptera: Aphididae) in sequential patches. *Journal of Insect Behaviour* 9, 683-694.
- de Moraes, C.M., Lewis, W.J. and Tumlinson, J.H. 2000. Examining plant-parasitoid interactions in tritrophic systems. *Anais de Sociedade Entomologica do Brasil* 29, 189-203.
- Pennacchio, F., Fanti, P., Falabella, P., Digilio, M. C., Biasaccia, F., Tremblay, E., 1999. Development and Nutrition of the Braconid Wasp, *Aphidius ervi* in Aposymbiotic Host Aphids. *Archives of Insect Biochemistry and Physiology* 40, 53-63.
- Pettitt, F.L., Loader, C.A. & Schon, M.K. 1994. Reduction of Nitrogen Concentration in the Hydroponic Solution on Population Growth Rate of the Aphids (Homoptera: Aphididae) *Aphis gossypii* on Cucumber and *Myzus persicae* on Pepper. *Environmental Entomology* 23, 930-936.
- Poppy, G.M. 1997. Tritrophic interactions: Improving ecological understanding and biological control? *Endeavour* 21, 61-65.
- Powell, W., Pennacchio, F., Poppy, G.M. & Tremblay, E. 1998. Strategies involved in the location of hosts by the parasitoid *Aphidius ervi* (Hymenoptera : Braconidae : Aphidiinae). *Biological control* 11, 104- 112.
- Price, P.W., Bouton, C.E., Gross, P., McPheron, B.A., Thompson, J.N., and Weis, A.E. 1980. Interactions among three trophic levels: Influence of Plants on Interactions Between Insect Herbivores and Natural Enemies. *Ann. Rev. Ecol. Syst.* 11, 41-65.
- Quicke, D.L. 1997. *Parasitic wasps*. Chapman & Hall, London, UK.
- Quoilin, J. 1966. Relations existant entre le potentiel de multiplication de *Myzus persicae* Sulz. (Homoptera – Aphididae) et la nutrition minérale de la plante-hôte par de solutions ioniquement équilibrées. *Bulletin des Recherches Agronomiques de Gembloux* 1, 140-152.
- Quoilin, J. 1967. Nutrition minérale de la plante-hôte et fécondité de *Myzus persicae* Sulz. (Homoptera – Aphididae). *Mededelingen van de Rijksfakulteit Landbouwwetenschappen te Gent* 32, 365-386.
- Rabasse, J-M. & van Steenis, M.1999. Biological Control of Aphids. In: *Integrated Pest and Disease Management in Greenhouse Crops*, eds. Albajes, R., Gullino, M.L., van Lenteren, J.C. and Elad, Y., Kluwer Academic Publishers, Dordrecht, The Netherlands, 235-243 pp.
- Rahier, M. 1978. Performance of *Myzus persicae* and production of its host plant, *Brassica rapa*, related to plant mineral nutrition. *Entomologia Experimentalis et Applicata* 24, 421-424.
- Ramakers, P.M.J. 1989. Biological Control in Greenhouses, In: *World Crop Pests, 2C, Aphids Their Biology, Natural Enemies and Control*, eds. Minks, A.K. & Harrewijn, P., Elsevier, Amsterdam, The Netherlands, 199-208 pp.
- Reed, D.K., Kindler, S.D. & Springer, T.L., 1992. Interactions of Russian wheat aphid, a hymenopterous parasitoid and resistant and susceptible slender wheatgrasses. *Entomologia Experimentalis et Applicata* 64, 239-246.
- Salt, G. 1938. Experimental studies in insect parasitism. VI, Host suitability. *Bulletin of Entomological Research* 29, 223-46.
- Schepers, A. 1989. Chemical Control, In: *World Crop Pests, 2C, Aphids Their Biology, Natural Enemies and Control*, Minks, A.K. & Harrewijn, P., Elsevier, Amsterdam, The Netherlands, 89-122 pp.
- Scriber, J.M. & Slansky, F., Jr. 1981. The nutritional ecology of immature insects. *Annual Review of Entomology* 26, 183.
- Sequeira, R. & Mackauer, M. 1992. Nutritional ecology of an insect host-parasitoid association: the pea aphid-*Aphidius ervi* system. *Ecology* 73, 183-189.
- Stadler, B. & Mackauer, M.1996. Influence of plant quality on interactions between the aphid parasitoid *Ephedrus californicus* Baker (Hymenoptera:Aphidiidae) and its host, *Acyrtosiphon pisum* (Harris) (Homoptera:Aphididae). *The Canadian Entomologist* 128, 27-39.
- Stapel, J.O., Cortesero, A.M., de Moraes, C.M., Tumlinson, J.H. & Lewis, W.J. 1997. Extrafloral nectar, honeydew, and sucrose effects on searching behavior and efficiency of

- Microplitis croceipes (Hymenoptera: Braconidae) in Cotton. *Environmental Entomology* 26, 617-623.
- Sary, P. 1974. Taxonomy, origin, distribution, and host range of *Aphidius* species (Hym., Aphidiidae) in relation to biological control of the pea aphid in Europe and North America. *Zeitschrift für Angewandte Entomologie* 77, 141-171.
- Sary, P. 1988. Natural enemies. In: *World Crop Pests, 2B, Aphids Their Biology, Natural Enemies and Control*, eds. Minks, A.K. & Harrewijn, P., Elsevier, Amsterdam, The Netherlands, 171-184 pp.
- Trädgårdsräkningen 2000, 2000. *Statistiska meddelanden, JO 36 SM 0001*. ISSN 1404-5834.
- Sting 25, 2003. *Newsletter on biological control in greenhouse*.
- Takada, H., Tada, E., 2000. A comparison between two strains from Japan and Europe of *Aphidius ervi*. *Entomologia Experimentalis et Applicata* 97, 11-20.
- Thurston, R. 1970. Toxicity of Trichome Exudates of *Nicotiana* and *Petunia* Species to Tobacco Hornworm Larvae. *Journal of Economic Entomology* 63, 272-274.
- Waring, G.L., Cobb, N.S., 1992. The impact of plant stress on herbivore population dynamics. In: *Insect Plant Interactions, Vol. IV*, ed. Bernays, E.A., Ed CRC Press, Florida, USA, 167-226 pp.
- Verkerk, R.H.J., Leather, S.R. & Wright, D.J. 1998. The potential for manipulating crop-pest-natural enemy interactions for improved insect pest management. *Bulletin of Entomological Research* 88, 493-501.
- Vet, L.E., Dicke, M. 1992. Ecology of infochemical use by natural enemies in a tritrophic context. *Annual Review of Entomology* 37, 141-172.
- Villagra C.A., Ramirez C.C. & Niemeyer H.M. 2002. Antipredator responses of aphids to parasitoids change as a function of aphid physiological state. *Animal Behaviour* 64, 677-683.
- Wilbert, H. 1967. Mechanische und Physiologische abwehrreaktionen einiger blattlausarten (Aphididae) gegen schlupfwespen (Hymenopterae). *Entomophaga* 12, 127-137.
- Williams, I.S. 1999. Slow-growth, high-mortality – a general hypothesis, or is it? *Ecological Entomology* 24, 490-495.
- Vinson, S.B. and Barbosa, P. 1987. Interrelationships of nutritional ecology of parasitoids. In: *Nutritional Ecology of Insects, Mites, and Spiders and related invertebrates*, eds., Slansky, F. & Rodrigues, J.G., John Wiley & Sons, New York, USA, 673-695 pp.
- Vinson, S.B. & Iwantsch, G.F. 1980. Host suitability for insect parasitoids. *Annual Review of Entomology* 25, 397-419.
- Woolridge, A.W. & Harrison, F.P. 1968. Effects of Soil Fertility on Abundance of Green Peach Aphids on Maryland Tobacco. *Journal of Economic Entomology* 61, 387-391.
- Völkl, W. & Mackauer, M., 2000. Oviposition behaviour of Aphidiine wasps (Hymenoptera: Braconidae, Aphidiinae): morphological adaptations and evolutionary trends. *The Canadian Entomologist* 132, 197-212.

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