BIOLOGICAL CONTROL OF WHITEFLY ON *GERBERA*:

SUCCESS OR FAILURE?

TRITROPHIC INTERACTIONS

BETWEEN *GERBERA JAMESONII*,

TRIALEURODES VAPORARIORUM AND *ENCARSIA FORMOSA*

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Tritrophic Interactions between *Gerbera jamesonii, Trialeurodes vaporariorum* and *Encarsia formosa*

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Für meine Eltern

...die Urheber der Gaben steigen wiederholt vor der Einbildungskraft hervor, man verknüpft mit ihrem Bilde eine angenehme Erinnerung, macht sich den Undank unmöglich und ein gelegentliches Erwidern leicht und wünschenswert.

(J.W. Goethe, Dichtung und Wahrheit)

8. Het maatschappelijke aanzien van een beursmakelaar heeft in de loop van de laatste eeuw ten onrechte een fundamentele wijziging ondergaan.
("With an evening coat and a white tie anybody, even a stockbroker, can gain a reputation for being civilised." Oscar Wilde, 1891. The Picture of Dorian Gray.)

9. De mythe van het zaligmakende moederschap staat het daadwerkelijke geluk van de 'verse' moeder vaak in de weg.

10. Wie het 'erfgoed' van Kaiser Wilhelm II aan de Nederlandse staat niet als Nederlands cultureel erfgoed kan zien heeft weinig historisch besef en dient derhalve geen onomkeerbare beslissingen op het cultuurhistorisch terrein te nemen.

11. Gezien het feit dat Rome het grootste openluchtmuseum ter wereld is, gespecialiseerd in onvervangbare kunst- en cultuurschatten, zou autoverkeer in het historische centrum van die stad verboden moeten zijn, in tegenstelling tot de mening van veel (autofiele) Romeinen.

12. Die grosse Zeitspanne, die 'Wessies' zur Vergangenheitsbewältigung benötig(t)en, müsste zur besseren Unterstützung von 'Ossies' bei der Auseinandersetzung mit ihrer Geschichte führen und zu mehr menschlichem Verständnis.

13. Schwestern sind im Leben einer Frau wie das Salz in der Suppe.
(Currer Bell (Charlotte Brontë), 1850. Biographical Notice of Ellis and Acton Bell. Preface to a reprint of Emily Brontës 'Wuthering Heights';
Tessa de Loo, 1993. De tweeling. De Arbeiderspers, Amsterdam;
Erich Kästner, 1924. Das doppelte Lottchen;)

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Susanne Sütterlin, Wageningen, 23 oktober 2000

STELLINGEN

1. In tegenstelling tot de duidelijk verticale, naar boven gerichte beweging in groentegewassen, vertonen wittevliegadulten een horizontale beweging op *Gerbera*. Daardoor komen de adulten uiteindelijk op het jonge blad in het hart van de plant terecht en vliegen ze niet snel weg uit het gewas, hetgeen op grond van eerder onderzoek werd verondersteld.
   (Van Lenteren, van Roermund & Sütterlin, 1996. Biological Control 6, 1-10.
   Dit proefschrift)

2. *Encarsia formosa* is vóór het landen op een plant niet in staat met gastheren geinfecteerde bladeren te onderscheiden van niet-geïnfecteerde bladeren, ondanks de andersluidende conclusies van Guerrieri (1997).
   (Guerrieri, E., 1997. Entomologia Experimentalis et Applicata 82: 129-133.
   Dit proefschrift)

3. Ontwikkelingsduur en fecunditeit van kaswittevlieg verschillen niet alleen tussen gewassen, maar - en dat was eerder juist niet gevonden door Dorsman & v.d. Vrie - ook in belangrijke mate tussen *Gerbera* cultivars. Dit maakt onderzoek naar waardplantresistentie tegen kaswittevlieg een nuttig en noodzakelijk onderdeel bij het ontwikkelen van een geïntegreerd bestrijdingsprogramma.
   (Dorsman & van de Vrie, 1887 Bull. IOBC/WPRS X/2, 46-51.
   Dit proefschrift)

4. De Nederlandse tuinbouwsector zou er goed aan doen, rassen en selecties van gewassen meer te toetsen op resistentie tegen insecten.
   (Sütterlin, 1999. Breeding for Resistance to Insects and Mites. IOBC/WPRS Bulletin 22(10), 53-58.)

5. Het meten van waardplantresistentie tegen insecten in een toets ten behoeve van de veredelaar, vermeerderaar en teler, dient op intacte planten met vrij bewegelijke insecten te gebeuren en niet op bladponsjes met insecten in kooitjes.
   (Balkema-Boonstra, Zijlstra & van der Helm, 1999
   Sütterlin & Butôt, 1999, Proc. Exper. & Appl. Entomology 10, 125-130)

6. De huidige politieke strijd over het al dan niet uitstellen van het verbod op het gebruik van een aantal chemische gewasbeschermingsmiddelen had een andere dimensie gekend, wanneer de landbouwsector in de afgelopen vijf jaar meer onderzoek naar de ontwikkeling van alternatieven had gefinancierd.
   (Uitzending discussieprogramma Radio 1, woensdag, 30 augustus 2000, 19.00 uur)

7. Ook met een iele gestalte en zeer weinig haar kun je 'Macho' worden genoemd.
   (Dit proefschrift)

CONTENTS

CHAPTER 1

INTRODUCTION

INTRODUCTION

In this thesis fundamental and applied research is described that was initiated to develop biological control of whitefly in the ornamental, *Gerbera jamesonii* Hook (Campanulales: Compositae). Before presenting the research objectives, general background information on the biology of the pest insect *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae), its natural enemy *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) and the target crop is provided.

THE GREENHOUSE WHITEFLY - ***Trialeurodes vaporariorum***

BIOLOGY

About 1200 whitefly species have been described, but the total number of species is assumed to be even higher (Bink-Moenen and Mound, 1990; Mound and Halsey, 1978). Whiteflies occur in tropical as well as in temperate zones and in many different habitats, such as forest, desert and chaparral. Of all whitefly species, only few are known to be pests. Two whitefly species frequently occur as pests in protected crops (Byrne et al., 1990): the greenhouse whitefly, *T. vaporariorum*, and the sweet potato or tobacco whitefly, *Bemisia tabaci*, biotype B, also referred to as silverleaf whitefly, *B. argentifolii* (Perring et al., 1993). Both species are highly polyphagous herbivores, occur worldwide and cause serious economic losses (Gerling, 1990).

Information on the biology and bionomics of whiteflies is presented by Gerling (1990), Gerling and Mayer (1996) and Byrne and Bellows (1991). A comprehensive summary of demographic data of the greenhouse whitefly can be found in van Roermund and van Lenteren (1992).

The selection of host plants by greenhouse whitefly before landing seems to be largely a random process. Although they show colour preferences (yellow-green spectrum), they do not necessarily land on the most suitable host plant. Whiteflies do not appear to use olfactory cues in host plant selection at a distance. They can distinguish between species and cultivars of host plants only after landing on them, and primarily by probing the plant tissue. Although the greenhouse whitefly is very polyphagous, clear oviposition preferences for certain plant species and cultivars exist (van Lenteren and Noldus, 1990). Within a plant, whiteflies prefer young leaves for feeding and oviposition. They reach the younger leaves as the result of a sequential process of alighting, probing, taking off, and moving upward. The preferences for certain plant species are persistent. On bad host plants frequent probing occurs and whiteflies soon take off. In contrast, on a good host plant no take-offs were observed and probing and feeding started almost immediately (van Lenteren et al., 1996). Host plant preference is positively correlated with population growth of whiteflies (van Lenteren and Noldus, 1990). Longevity of adult whiteflies can be considerable (maximally up to several months) and oviposition may occur over a period longer than the time needed for immature development. Thus, overlapping generations occur and patches of infestation gradually increase. As a result of the between and within host-plant selection processes, greenhouse whiteflies are distinctly and very strongly aggregated at various spatial levels in the crop (Noldus et al., 1986; Martin et al., 1991). Life history parameters such as development time, immature mortality and fecundity of whitefly differ greatly between plant species (van Roermund and van Lenteren, 1992).

DAMAGE

Damage caused by whiteflies can be grouped into three categories (e.g. Byrne et al., 1990).

(1) Direct damage by consuming transportable carbohydrates causing chlorotic spots, leaf shed and reduced growth. This is reported for example for *T. vaporariorum* on tomatoes (Byrne and Bellows, 1991; Lindquist et al., 1972).

(2) Honeydew and sooty mould contamination of plant leaves and harvestable products. In protected crops, vegetables as well as ornamentals, the contamination with honeydew and sooty moulds caused by *T. vaporariorum* is considered to be the most important kind of plant damage. Yield reductions due to honeydew and sooty mould in tomato are only caused at a relatively high average pest density of 70 immatures/cm^2 (Hussey et al., 1969). However, contamination of fruits by honeydew is reached after a much lower whitefly infestation, and in ornamentals, where leaves are sold with the flowers, reduced marketability or even unacceptable market quality is reached with a few nymphs per leaf (Byrne et al., 1990).

(3) Pathogen transmission by whiteflies. Bacterial, fungal and viral pathogen transmissions do occur. Economically most important in annual cropping systems is virus transmission. Among the transmitted viruses an important group are bigemini viruses (Geminiviridae), i.e. Cotton leaf crumple virus (CLCrV), Tomato yellow leaf curl virus (TYLCV) or Abutilon mozaik virus (AbMV). Among other vectors whiteflies are also known to transmit some Badnaviridae and Potyviridae (Brunt et al., 1996). *T. vaporariorum* transmits beet pseudo-yellows virus (BPYV), belonging to the Closteroviridae. The main virus transmission vector is *B. tabaci*. In Europe, few reports of virus transmission by whiteflies in protected crops have been published up to now, in Spain and France BPYV transmitted by *T. vaporariorum* in cucumber has very recently been displaced by cucurbit yellow stunting disorder virus (CYSDV) which is transmitted by *Bemisia tabaci* B-type (Berdiales et al., 1999). The major threat is suggested to be *B. tabaci* B-type (or *B. argentifolii*) in specific ornamental crops like poinsettia (Perring et al., 1993; Heinz and Parella, 1994).

WHITEFLY MANAGEMENT STRATEGIES

In natural ecosystems and agroecosystems where pesticides are not used, an array of natural enemies usually keeps whiteflies at low numbers: predators, parasitoids and pathogens are all of large influence. Studies in two cropping systems, tomatoes in the 1960s in California and cotton during the period 1925-1992 in Sudan, has shown that whiteflies can be kept under perfect *natural control* (van Lenteren et al., 1996). However, when pesticides are applied, natural enemies are exterminated resulting in whitefly pest outbreaks, in the above mentioned cases *T. vaporariorum* and *B. tabaci*, respectively.

In protected crops, especially in ornamentals, the low tolerance of pest insects is reflected by widespread and frequent use of insecticides. Nowadays, the risks to man and environment and the problem of development of resistance against insecticides by insects (Dittrich et al., 1990) are recognized and alternatives are being considered. Already years ago, development of resistance to certain pesticides is reported of *T. vaporariorum* and *B. tabaci*, as well as acceleration ('resurgence') of whitefly populations through chemicals (Wardlow et al., 1972; Dittrich et al., 1985). Therefore, non-chemical control methods of whitefly pests are being looked for. Monitoring of whiteflies is used to trace the insects in a crop and to keep a record of their presence. Alternative control methods are, for example, integrated pest management and breeding for host plant resistance to insects. Biological control of whitefly, an element of integrated pest management, may offer a possibility and several strategies can be followed (van Lenteren et al., 1996):

(1) The inoculative release method. Beneficial organisms are collected in a region from which the pest insect originates and introduced in relatively small numbers in a region where the pest was introduced. The aim is a long term control effect and the method has been successful when a continuous existence of the natural enemy was possible (Onillon, 1990). An example is given by Smith et al. (1964) for the control of citrus blackfly by *Encarsia clypealis* in humid regions of Mexico.

(2) The inundative release method. Beneficials are released periodically in large numbers in a crop for immediate control. This requires mass rearing of the natural enemy. Illustrating examples are the release of *Encarsia formosa* against *B. tabaci* in poinsettia and the application of entomopathogenic fungi against *T. vaporariorum* (Albert, 1990; Fransen, 1990).

(3) The seasonal inoculative release method. This method differs essentially from the above mentioned inundative releases in the fact that a buildup of the natural enemy population for control later during the same season is pursued. Thus, it requires several generations of natural enemies and pest insects in a crop. The approach is succesfully applied in the control of *T. vaporariorum* by *E. formosa* in protected tomato crops (van Lenteren and Woets, 1988).

*THE PARASITOID - **Encarsia formosa***

BIOLOGY

The genus *Encarsia* contains about 150 species of parasitoids, but probably more will be found in future. The females develop in hosts belonging to the Diaspididae and Aleyrodidae. The species show a wide variety in reproductive behaviour (Gerling, 1990). Some of the species, like *E. formosa*, are primary thelytokous parasitoids, i.e., females are produced on a phytophagous host insect parthenogenetically. Other *Encarsia* species are also primary parasitoids, but produce males from unfertilized eggs and females from fertilized eggs, i.e., they are arrhenotokous. Still other species are arrhenotokous hyperparasitoids and produce males and females by laying eggs in other, immature parasitoids of a different species. Further, species are known where one sex, usually the female, develops as a primary parasitoid, and the other sex develops hyperparasitically on their own or another species of parasitoid, i.e., heteronomous hyperparasitoids or facultative autoparasitoids (van Lenteren et al., 1996).

Fundamental research has provided information on how the parasitoid locates and attacks hosts. No experimental proof that *E. formosa* is able to locate infested plants from a distance was found after ample efforts. Searching is random on all levels, and after a host has been found the search pattern does not alter, e.g. from random into area restricted search. The only important change in foraging behaviour which was observed is that, in comparison with search times on an uninfested leaf, a parasitoid keeps searching considerably longer (2 to 10 times) on a leaf once a whitefly larva was found or when other indicators of whitefly presence were discovered, e.g. honeydew, exuviae, dead hosts, (van Lenteren et al., 1996).

The ecology of *E. formosa* is reviewed, among others, by Noldus and van Lenteren (1990). Demographic data were collected by van Roermund and van Lenteren (1992).

BIOLOGICAL CONTROL OF THE GREENHOUSE WHITEFLY WITH ***E. formosa***

In glasshouses in the United Kingdom *T. vaporariorum* was found and described for the first time in 1856 by Westwood (Westwood, 1856). The species is supposed to originate and to be imported from Mexico on Orchidaceae into Europe. In 1926, a tomato grower in England drew the attention of the entomologist Speyer to black pupae among the normally white ones of *T. vaporariorum*. From the black pupae parasitoids emerged that were identified as *E. formosa* (Speyer, 1927). In a few years time an Experimental Research Station in the UK was annually supplying 1.5 million wasps for whitefly control to approximately 800 nurseries in the country. Many millions of parasitoids were sent to other countries in Europe, Canada, Australia and New Zealand. However, biological control stopped shortly after World War II, when synthetic organic pesticides provided control in most protected crops. Since the early seventies, the interest in biological control of whitefly pests has been renewed. Due to resistance against several pesticides, whitefly populations reached epidemic proportions and alternative control methods had to be found. The development of biological and integrated control programmes in protected crops during the 70ties was possible, because of the already known efficacy of *E. formosa* as natural enemy against the greenhouse whitefly (van Lenteren et al., 1996). During the past 25 years, over 30 species of natural enemies have been identified and introduced against 20 pest species in greenhouses (van Lenteren and Woets, 1988; van Lenteren, 1995). Presently biological control of the greenhouse whitefly with *E. formosa* is applied on an area of almost 5000 ha, and is used in more than 20 out of the 35 countries that have a glasshouse industry. The parasitoid is released mainly in Europe on vegetable crops like tomato and cucumber (van Lenteren, 1995). The positive spin-off is reduced environmental pollution, a healthier work environment for growers and consumer appreciation of produce with less or no chemical residues.

BIOLOGICAL CONTROL ON ORNAMENTALS

The use of biological control against whiteflies on ornamental crops has been suggested for years (e.g. Helgesen and Tauber, 1974; Nucifora and Calabretta, 1986; Albert, 1990; Benuzzi et al., 1990; Enkegaard, 1993; Stenseth, 1993), but is still relatively little practised today. Biological control in ornamentals is mostly used in Europe (Blümel, 1996; Fransen, 1996). The limited use of biological control can be explained by the phenomenon of a much lower tolerance level for whiteflies in ornamental crops due to harvesting leaves together with flowers and, for instance in the Netherlands, export restrictions resulting in the so-called zero tolerance for pest organisms. Under such conditions, biological control and IPM are difficult to apply. However, experience with biological control in vegetable crops indicate that the common belief that chemically treated crops contain a priori fewer pest organisms than biologically controlled ones is not correct (van Lenteren, 1995). Also, the widespread reliance on insecticides and their frequent application in ornamentals hold a greater risk of the development of resistance of insects against pesticides than in vegetables, where insecticides are less applied (Dittrich et al., 1990).

The problem of insecticide resistance, besides the risks for man and environment, was recognized recently at the policy level in the Netherlands. The Dutch government decided to launch a 'Multi Year Crop Protection Program' (MJP-G, 1991), which aims at the reduction of the overall use of pesticides in agriculture and horticulture by at least 50 % in the year 2000, compared to figures from 1984. The program also stimulated research for other control methods in protected ornamentals, among which biological and integrated pest and disease management.

The IOBC/WPRS Working Group 'Integrated Control in Glasshouses' concluded in 1987 that biological control in ornamentals lagged far behind that in vegetables. A workshop was organized to identify the most important pest problems in ornamentals; and the most promising pests and crops for development and application of biological control were identified (van Lenteren and Wardlow, 1989). This effort certainly resulted in more research on the topic, much of which was published in the last four volumes of IOBC-Bulletins of this working group: IOBC/WPRS 1990; 1993; 1996; 1999. All together 72 papers appeared on biological and integrated control in ornamentals.

THE HOST PLANT ***Gerbera jamesonii***

The genus *Gerbera* has a large region of origin: from Southern Africa, Madagaskar and India towards Nepal, China and areas in Siberia and Tasmania.

More than 20 species were already known, when in 1887 the species *G. jamesonii* was brought to the UK by Jameson (Penningsfeld and Forchthammer, 1980). Breeding soon led to numerous cultivars, differing in flower colour and size, etc., but also in leaf size, -structure and -hairiness. Each year new cultivars are introduced by plant breeders. For example, in 1997, 62 new cultivars have been introduced on the Dutch market (Anonymous, 1998a).

Production of cut flowers and plants under glass involved an area of 5556 ha in 1996 in the Netherlands. The turnover of Dutch cut flowers was valued on 4.3 billion Dutch guilders in 1997 (Anonymous, 1998a). *G. jamesonii* crops were produced on approximately 235 ha in 1997/1998 (Anonymous, 1998b). The auction turnover was 201 million Dutch guilders in 1999 (Anonymous, 2000), which makes *Gerbera* the fifth cut flower in the top ten of the Dutch cut flower turnover (Anonymous, 2000).

*BIOLOGICAL CONTROL OF WHITEFLY ON **G. jamesonii***

In most ornamental crops where flowers are marketed together with leaves, the tolerance of injury by pests is practically zero. At Dutch auctions, a so-called zero tolerance for insect damage and presence of insects is required only for export to certain countries (Fransen, 1993). However, this has become the 'standard' for all products, because growers then get the highest price for their material. *G. jamesonii* is an ideal model crop for trying out biological control programs in protected ornamental plants, as only the flowers are harvested and low numbers of insects present on the leaves can be tolerated as long as the flowers are not injured. Whiteflies normally occur only on the leaves of gerbera and, therefore, development of biological control of this pest seemed to offer realistic opportunities.

RESEARCH OBJECTIVES AND HYPOTHESES

In *G. jamesonii* crops, whiteflies are among the main insect pest species (Dorsman and van de Vrie, 1987). Biological control of greenhouse whitefly in this crop has been under study for a decade (Dorsman and van de Vrie, 1987; van de Vrie, 1989; Blümel, 1992; Benuzzi and Nicoli, 1993; Albert et al., 1993; Ravensberg and Altena, 1993). Experience with biological control on vegetables (tomato, cucumber) with *E. formosa* was an important trigger for this research on *Gerbera*. However, mostly 'trial and error' methods have been used to determine introduction schemes, and these trials to control whitefly in *G. jamesonii* crops with *E. formosa* gave ambiguous results (Nucifora and Calabretta, 1986; Blümel, 1992; Benuzzi and Nicoli, 1993).

The main objective of this research was, therefore, to obtain understanding of the tritrophic relationship *G. jamesonii, T. vaporariorum* and *E. formosa* by an in-depth study on the biology and behaviour of the pest insect and its natural enemy, and, as a result, to be able to judge whether biological control of *T. vaporariorum* on *G. jamesonii* can be a realistic option.

The interactions between the three trophic levels are manyfold and complex

(Figure 1). As in most ornamentals, there are many different cultivars of *G. jamesonii* grown commercially. Plant characteristics such as colour, shape, structure, smell and taste vary to a large extent and may grossly influence the relationship with the other two trophic levels. Whitefly feeding on *Gerbera* can be reduced by inherited cultivar qualities that result in less damage to the plant (plant resistance). Also plant cultivars can possess the ability to withstand or recover from damage (tolerance) caused by the feeding insect (Smith, 1989).

The knowledge about the tritrophic system *G. jamesonii*, *T. vaporariorum* and *E. formosa* before this project was started, can be summarized as follows:

(1) Life history parameters of the greenhouse whitefly (development time, mortality, total fecundity) were determined for a number of *G. jamesonii* cultivars, and these cultivars appeared to have the same host plant quality for *T. vaporariorum*. The suitability of *Gerbera* for the greenhouse whitefly and the population growth rate were similar to that on the vegetable host plant tomato (Dorsman and van de Vrie, 1987; Dorsman and van de Vrie, unpublished). This means that the host plant quality of *G. jamesonii* for *T. vaporariorum* is relatively poor when compared with cucumber and sweet pepper.

(2) Cultivar characteristics, such as leaf size and leaf surface structure, vary substantially in *G. jamesonii*. Such characteristics may influence the behaviour and the performance of the parasitoid, as is shown for *E. formosa* on cucumber varieties with differences in leaf hairiness. Van Lenteren et al. (1995) showed that with increasing hairiness of cucumber cultivars, the searching efficiency of *E. formosa* decreased.

(3) The plant architecture of *G. jamesonii* differs a lot from vegetable host plants (tomato, cucumber) of *T. vaporariorum*. This might influence the distribution of whiteflies and the host searching by *E. formosa*.

The working hypotheses of this research are that (1) the rosette type host plant shape of *G. jamesonii* leads to a whitefly dispersal and distribution that is different from that on vegetables such as cucumber and tomato, (2) the host plant architecture and leaf hairiness of *G. jamesonii* negatively influence the searching behaviour of the parasitoid *E. formosa* for its host *T. vaporariorum* and (3) these characteristics taken together may result in difficult or impossible biological control of *T. vaporariorum* on *G. jamesonii*.

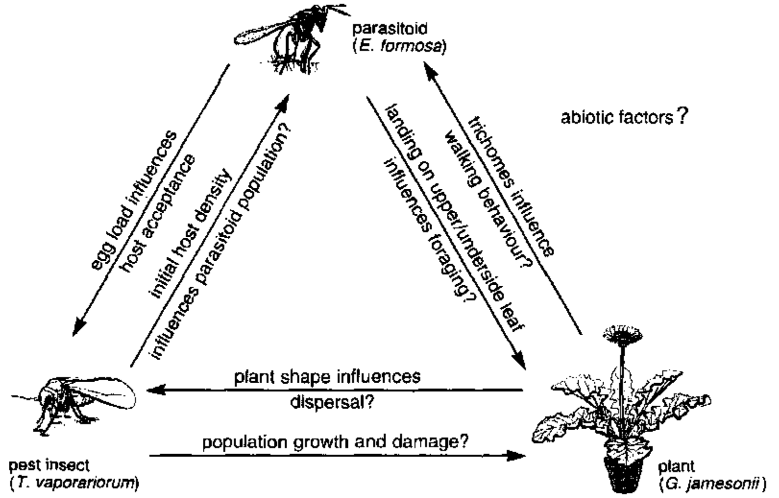

Figure 1. Tritrophic interactions between *Gerbera jamesonii*, *Trialeurodes vaporariorum* and *Encarsia formosa*. Interactions which were studied as part of the research hypotheses are indicated.

OUTLINE OF THE THESIS

Dispersal and host plant searching behaviour of *T. vaporariorum*

To test our hypothesis that host plant architecture of *G. jamesonii* results in a different whitefly distribution pattern when compared with vegetables such as tomato and cucumber, we started studying whitefly dispersal behaviour and the choice of oviposition and feeding sites of the greenhouse whitefly within a plant. The behaviour of the herbivore was compared on two cultivars of *G. jamesonii*, differing in hairiness (**chapter 2**). Three parameters (development time, mortality and fecundity) to measure performance of *T. vaporariorum* were investigated to determine a possible link with preference for certain leaves or cultivars by whitefly adults (**chapter 2, 8**). The dispersal and aggregation of whitefly adults between plants was investigated next and this is described in **chapter 3.**

Searching behaviour of *E. formosa* on *G. jamesonii*

The influence of hairiness of different plant cultivars on the walking behaviour of the parasitoid *E. formosa* is discussed in **chapter 4**. The effect of plant architecture of *G. jamesonii* on the searching behaviour of the parasitoid before and after landing on the plant is described in **chapter 5**. In **Chapter 6** details are given on the foraging behaviour of *E. formosa* on leaves of a range of *Gerbera* cultivars differing in hairiness, and a comparison with foraging on tomato is made.

Population dynamics of herbivore and parasitoid in glasshouses

Glasshouse studies are essential to validate the conclusions based on small population experiments and laboratory experiments. Therefore, the effect of introduction of different numbers of *E. formosa* on the control of *T. vaporariorum* was tested in three experimental glasshouses during an 11-week observation period (**chapter 7**). Also, population development of greenhouse whitefly and its parasitoid on *G. jamesonii* was observed on a semi-commercial scale in a glasshouse during a 150 days period (**chapter 8**).

Simulation model and sensitivity analysis

A simulation model of the tritrophic relation *G. jamesonii*, *T. vaporariorum* and *E. formosa* was developed and validated with glasshouse experiments (**chapters 7** and **8**). Finally, the results of a sensitivity analysis, concerning the influence of (i) the release strategy, (ii) the plant cultivar on the life history of the herbivore, (iii) the total leaf area on the searching behaviour of the parasitoid and (iii) the temperature on the model system of *G. jamesonii* - *T. vaporariorum* - *E. formosa* was performed to trace potential explanations for success or failure of biological control of *T. vaporariorum* in *Gerbera* (**chapter 8**).

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CHAPTER 2

DISPERSAL AND DISTRIBUTION OF GREENHOUSE WHITEFLIES ON THE ORNAMENTAL *GERBERA JAMESONII*: STUDIES AT PLANT LEVEL

SUBMITTED AS:
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DISPERSAL AND DISTRIBUTION OF GREENHOUSE WHITEFLIES ON THE ORNAMENTAL *GERBERA JAMESONII*: STUDIES AT PLANT LEVEL

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STUDIES AT PLANT LEVEL

ABSTRACT

On the ornamental plant *Gerbera jamesonii* the dispersal process of whiteflies is directed to the centre of the plant. This leads to adult and egg aggregating on young leaves, on hairy as well as on non-hairy cultivars. About 80 % of the recently emerged adults move to the young leaves within a day. Females have a preference for feeding and ovipositing on young leaves. Performance, in terms of development time and immature mortality, was measured on leaves of three different age classes to determine a possible link with preference. Duration of development from egg to adult was similar on the three leaf age classes (22-23 days). However, immature mortality was higher on old and medium aged leaves (more than 65 %) compared to immature mortality on young leaves (44 %). Whiteflies appear to select those leaves for oviposition where the survival of their offspring is largest.

INTRODUCTION

The interaction of the polyphagous, phytophagous greenhouse whitefly, *Trialeurodes vaporariorum*, with its host plants and its parasitoid *Encarsia formosa* has been studied extensively on vegetables (e.g. Van Lenteren & Noldus, 1990, Noldus & van Lenteren, 1990, Van Lenteren et al., 1996). This has led to a reliable biological control method on major vegetable crops under commercial conditions (Van Lenteren & Woets, 1988). *T. vaporariorum* is also a prominent pest insect in ornamental crops. Different reasons, such as pesticide resistance, increasing costs of pesticides and governmental restrictions concerning extensive pesticide use, have led to a search for control of insect pests in ornamentals that is not based on chemicals. This trend is reported for the Netherlands and also worldwide (see Van Lenteren, 1990; Fransen, 1992; Albert et al., 1993; Benuzzi & Nicoli, 1993; and Ravensberg & Altena, 1993).
We choose to study the possibility for biological control of *T. vaporariorum* in the ornamental *Gerbera jamesonii*, because only the flowers are marketed and the presence of some injury or even insect can be tolerated on the leaves. To develop a reliable biological control method of the greenhouse whitefly on *Gerbera*, it is essential to know the relationships between the host plant, the herbivorous insect and its parasitoids (Price et al., 1980). *Gerbera* is not a very good host plant for *T. vaporariorum* in terms of life history parameters when compared to vegetable crops such as egg plant and cucumber (van Roermund & van Lenteren, 1992). The host-plant suitability for the whitefly does resemble that of tomato (van de Merendonk & van Lenteren, 1978; Dorsman & van de Vrie, 1987), a crop in which the greenhouse whitefly is easily controlled under glasshouse conditions.

However, *Gerbera* has a completely different plant architecture when compared to vegetables as tomato, cucumber or egg plant. The leaves of the plant are positioned in a horizontal spiral ("rosette"). The rosette shape of *Gerbera* may influence the dispersal behaviour of the whitefly. In several whitefly species, like *Aleyrodes brassicae, Bemisia tabaci* and *T. vaporariorum* an almost immediate upward vertical movement of the emerged adults in the host plant directed to the younger leaves was observed on different crops such as cabbage, cotton, cucumber, eggplant and tomato (El Khidir, 1963; Ohnesorge et al., 1980; Noldus et al., 1985; Xu Rumei, 1991). To reach the young leaves in a rosette type plant like *Gerbera*, a whitefly female would have to move horizontally to the centre of a plant. With a mainly upward movement, the adults would soon leave the canopy of such a crop and disperse more to other plants than in a vertical structured vegetable crop. They may even depart entirely from these rosette plants.

In addition to the difference in plant architecture with vegetable crops, another complicating factor is that a large variety of *Gerbera* cultivars exists, which differ in e.g. hairiness of the leaves (Sütterlin & van Lenteren, 1997). This trichome diversity can influence the dispersal behaviour of whitefly adults and therefore the distribution of a *T. vaporariorum* population in a crop (Van

Lenteren & de Ponti, 1990; Van Lenteren et al., 1995). Also survival of immatures may be influenced by differences in hair density.

The major questions addressed in this study are:
Does the within-plant movement of *T. vaporariorum* in *Gerbera* plants result in the same situation as in the vegetable crop tomato, i.e. is there movement of adult whiteflies to the younger leaves and is this the result of a preference for feeding and ovipositing on young leaves compared to the other leaf types?
If there is a preference by the adults for the young leaves for feeding and ovipositing on a rosette type plant, do we find the same preference when leaves are offered at one horizontal level?
How does leaf selection behaviour relate to whitefly performance?
Is the distribution and dispersal of the adult whiteflies different on *Gerbera* cultivars with different amount of hairs?

MATERIAL AND METHODS

Within-plant movement: For the first set of experiments ten intact, unsprayed *Gerbera* plants, and for the second set of experiments five intact, unsprayed plants of either the cultivar 'Terra Fame', hereafter referred to as 'Fame', or 'Parade' have been used. 'Parade' is a "hairy" cultivar with 340 trichomes/cm^2 leaf area and 'Fame' is a "less hairy" cultivar with 110 trichomes/cm^2 leaf surface and (Sütterlin and van Lenteren, 1997). The plants were uniform of size and age (16 weeks grown in a glasshouse, plants coming from meristem culture), in the six to eight leaf-stage. The leaves were classified into three age groups on a morphological basis, that is leaf shape and leaf texture: (i) young leaves, (ii) full grown or medium leaves and (iii) old leaves. The first and second leaves in the heart of the plants were categorized as young leaves, 2nd to 4th as medium leaves and the remaining two other ones as old leaves. The plants were placed on a table, 25 cm distance in between, in a glasshouse compartment of 2 x 3 m. Temperature was 21 ±1 °C in the first set of experiments and 23 ±1 °C for the second set. RH was about 60% and 70% and a photoperiod of 16L : 8D was set.

In the first set of experiments 25 or 50 adult whiteflies were released out of a glass vial at the stem of every plant. The adults were collected from a whitefly rearing (temperature 25 ±1°C and photoperiod 16L:8D), which had been kept on *Gerbera* (cv. 'Fame') for more than five generations, where the insects were taken randomly from the the young leaves of the plants. After the release of the adults, all the leaves were checked for the presence of whiteflies every hour. Numbers were recorded per plant and leaf. One last record was made 24 h after the release and the whiteflies were removed from the plants. The experiment was conducted three times for cv. 'Fame' and twice for cv. 'Parade'.

In a second experiment, a small piece (1.5 cm x 2.5 cm) of a *Gerbera* leaf full of whitefly pupae was pinned upon the underside of a medium leaf (on which emergence takes place) on each of the five plants used per experiment (Figure 1). The movement of the emerged adults was checked carefully on all leaves by sight with a hand mirror and recorded hourly from 6.00 a.m. to 10.00 p.m. (light period), for five to seven days. Adults on the leaf from which they emerged were removed after the first light period at 10.00 p.m. Adults that emerged the second day could therefore be recorded as well. At 10.00 p.m. on the second day the piece of leaf with pupae was removed. Also all whitefly adults observed on the young leaves were removed then. The number of adults is given as a total per leaf age class from all plants used per experiment. For both cultivars the experiment was conducted three times.

As almost no movement of adults was observed during the dark period in all experiments no detailed observations during the dark period were made.

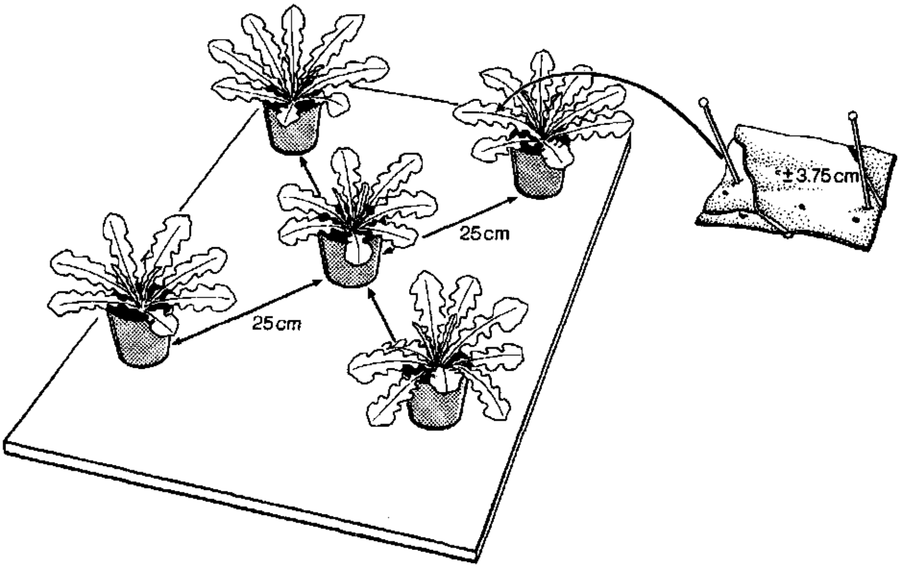

Figure 1. Dispersal experiment with newly emerged greenhouse whiteflies on *Gerbera*, cultivars 'Fame' and 'Parade'.

Choice of leaf age by adults: The influence of the host plant architecture (rosette) on the dispersal behaviour of whitefly females and on the choice of a feeding and oviposition site was investigated by placing the three leaf age classes of a plant at one horizontal level. In a black-coloured cage three glass vials with each a leaf of one of the three leaf ages of either the cv.'s 'Fame' and 'Parade' were placed at the same level in a semi-circle, 50 cm from a release point (Figure 2). We used leaves of plants that were 16 weeks old and in the six to eight leaf-stage. Leaves were carefully chosen for the leaf age classes of both cultivars, so that they had approximatly the same surface area. The position of leaves of all the age classes was shifted, to correct for site effects. In each replicate (18 replicates per cultivar) we released 25 whitefly females simultaneously from a glass vial. We observed the first flight from the release point and recorded the first landing ("first choice") on one of the leaves or elsewhere. Afterwards the distribution of females over the leaves was recorded six times during the light period and after 24 hours. All leaves were then checked for presence of eggs. The cage stood in a controlled-environment room with a constant temperature of 21 ±1 °C, a relative humidity of 60% and a photophase of 16 h.

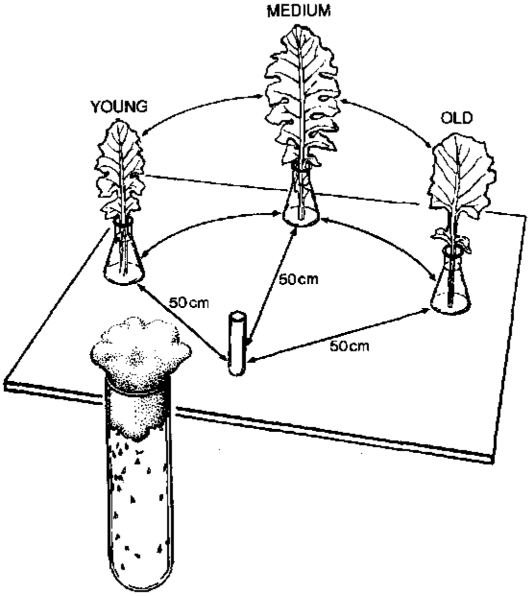

Figure 2. Leaf age choice experiment of greenhouse whitefly adults when leaves were offered at a horizontal level.

Egg to adult development of *T. vaporariorum* on *Gerbera*: *Gerbera* cv. 'Fame' was used for this experiment. The development of immature whiteflies was measured on young, medium and old leaves. Whitefly females were randomly taken from the *Gerbera* - whitefly rearing, and were 1 to 7 days old. They were put into leaf cages on the three different leaf types for 24 h in a glasshouse compartment of 20 °C and the number of females chosen was such that about 200 eggs were laid. However, with the old leaves the maximum number of eggs laid was only 66, although the same number of females were caged, as for the other leaf age classes. The plants were then placed into a climate room of 25 ±1 °C, a relative humidity of 60 to 70% and a photophase of 18 hours. All developing immatures were individually checked once a day until they either died or emerged as adults. The agreement between cumulative egg to adult development curves was tested with the Kolmogorov-Smirnov test (Siegel & Castellan, 1988).

RESULTS

Within-plant movement

First set of experiments: On cv. 'Parade' adult whiteflies moved to the young leaves. Already from the first observation, 20 minutes after release, the percentage adults alighting was largest, namely 43% and 50%, on young leaves (Figure 3). Both replicates gave statistically the same results (Mann Whitney U test, $P > 0.05$). The percentage adults increased on the young leaf type (Friedman Two-Way Analysis of Variance, $P << 0.001$) until the seventh hour and remained the same afterwards. On the medium and old leaves the percentage whiteflies decreased and remained similar 6 and 4 hours after release, respectively (Friedman, $P < 0.03$ and $P < 0.01$) (Figure 3). In all replicates and on both cultivars, the mean numbers of individuals per cm^2 after 24 h were higher on the young leaf than on the medium or old leaves (Table 1). On cv. 'Fame' we found 2.4 to 5.5 times more adults per cm^2 on the young leaves compared to the medium and old leaves, on cv. 'Parade' we found even 4.3 to 24.7 times as many adults per cm^2 on the young leaves compared to the other leaf age classes.

Table 1. Mean number of adult *Trialeurodes vaporariorum* per cm^2 leaf area on three leaf age classes on *Gerbera*, cv. 'Fame' and 'Parade' after a 24 h period.

	Cultivar 'Fame' mean ± SD			**Cultivar 'Parade'** mean ± SD	
Leaf age class	replicate 1	replicate 2	replicate 3	replicate 1	replicate 2
Young	0.029± 0.013	0.028± 0.013	0.022± 0.013	0.039± 0.018	0.074± 0.026
Medium	0.009± 0.007	0.007± 0.004	0.011± 0.007	0.007± 0.005	0.009± 0.006
Old	0.012± 0.018	0.006± 0.006	0.004± 0.005	0.009± 0.006	0.003± 0.003
Total leaf area (cm^2)	1022.7	1022.7	1022.7	1544.3	1923.6
No. of adults released	250	250	500	500	500
[1]No. of adults observed / h	122.8± 262.5	97.4± 207.6	157.7± 330.5	165.1± 121.2	166.6±122.3

[1]Total observation period; mean ± *SD*

When pupae instead of adults were introduced we observed the following: whiteflies only emerged after the lights were turned on. The number of whiteflies that emerged was statistically the same on both cultivars in the three experiments (Mann-Whitney W test, $P = 0.46$). Also on both cultivars, most of the insects had emerged during four hours after light on (Mann-Whitney W test, $P = 0.75$), after which movement away from the leaf of emergence started. The mean time of leaving this leaf, about nine hours after emergence, is for both cultivars statistically the same (Mann-Whitney W test, $P = 0.074$). The time that 50 % of the adult whiteflies left the leaf of emergence was larger on cv. 'Fame' compared to cv. 'Parade', in all three experimental replicates (Mann-

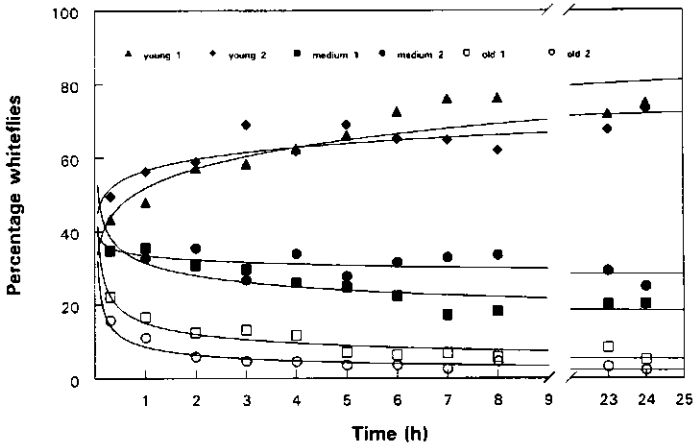

Figure 3. Distribution of *Trialeurodes vaporariorum* adults, expressed as percentage, over three leaf age classes during 24 hours on *Gerbera*, cv. 'Parade'. Whiteflies were introduced as adults on intact plants.

young 1; young 2 = adults on young leaves, replicate 1 and 2, respectively
medium 1; medium 2 = adults on medium leaves, replicate 1 and 2, respectively
old 1; old 2 = adults on old leaves, replicate 1 and 2, respectively

Table 2. The number of emerged whiteflies during the experiments, the time when the maximum number of adults was found on the leaves of emergence, the time when 50% of adults had left the leaf of emergence after starting the experiment, and the mean time of leaving, cv.'s 'Fame' and 'Parade'.

Experiment	No. of emerged adults[1] (mean ± *SD*)	Time max. emerged (h) # [1] (mean ± *SD*)	Time at which 50 % left leaf of emergence (h) [1] (mean ± *SD*)	Mean time of leaving (h) [1] (mean ± *SD*)
1 (Fame)	20.67a ± 11.02	3.17a ± 0.57	14.57a ± 3.39	11.07a ± 3.61
2 (Fame)	25.0a ± 15.56	5.0a ± 2.12	14.55a ± 2.05	9.55a ± 4.17
3 (Fame)	135.0a ± 31.19	3.63a ± 0.12	13.30a ± 1.37	9.67a ± 1.46
1 (Parade)	32.33a ± 15.53	3.17a ± 0.57	9.87b ± 0.95	6.70a ± 0.79
2 (Parade)	31.5a ± 16.26	5.3a ± 1.41	13.15b ± 2.62	7.85a ± 1.20
3 (Parade)	134.67a ± 30.35	3.63a ± 0.12	11.80b ± 1.40	8.17a ± 1.51

[1] Numbers followed by the same letter within a colum are not significantly different (Kruskal-Wallis test, $\alpha = 0.05$ for differences in the experiments per cultivar and Mann-Whitney W test, $\alpha = 0.05$ for differences between the cultivars).

Whitney W test, P = 0.016) (Table 2). A sharp increase of adults on the young leaves was seen about 8.5 h after the start of the experiment and the number of whiteflies continued to increase on that leaf type for several hours.

The distribution stabilized 13 h after the start of the experiment on the young leaves, until newly emerged whiteflies were able to alight on that leaf age class. The decrease of whitefly adults on the leaf of emergence is just ahead of the increase of whiteflies on the young leaves (Figure 4(a) and 4(b)).

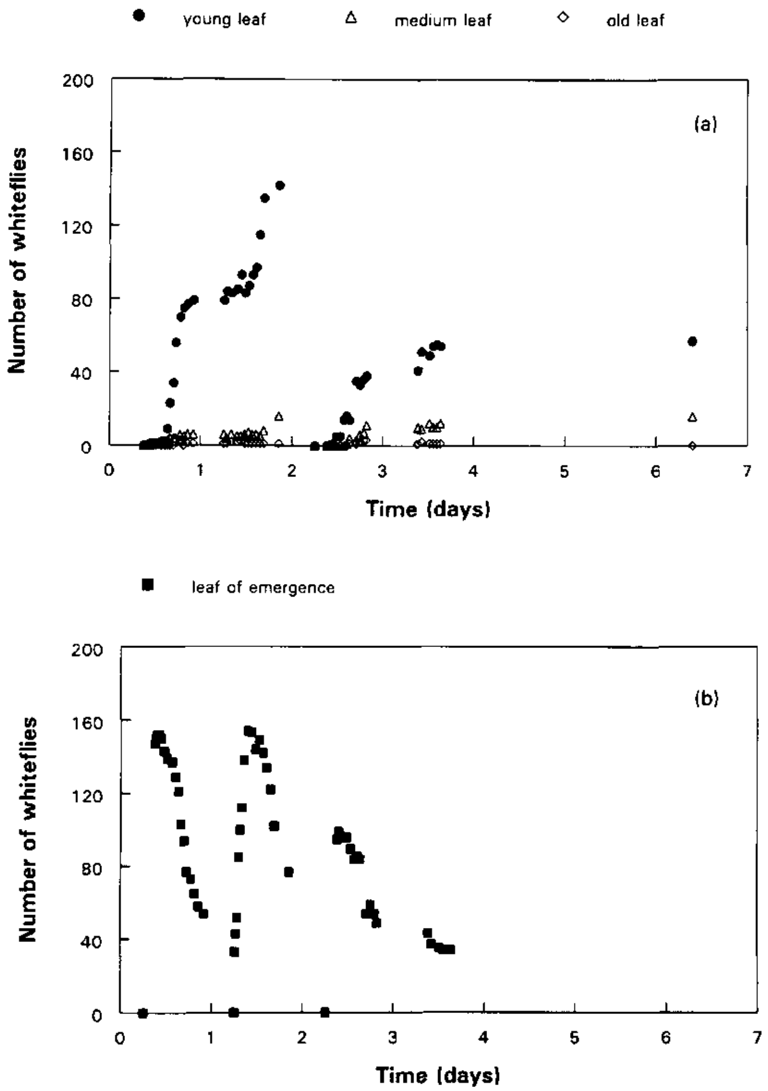

Figure 4. 4 a. Number of adult *Trialeurodes vaporariorum* on three leaf age classes during a seven day period on *Gerbera*, cv. 'Parade'. Observations were made on day 1 up to 5 and day 7.
4 b. The number of adults on the leaf of emergence during four days, whiteflies were removed from this leaf at the end of the experimental day. Whiteflies were introduced as pupae on a piece of leaf in the intact plant.

Leaf-age choice of adults for feeding and oviposition - leaves offered at one level.

The percentages of females landing on the three leaf age classes after the first flight and after 24 h, the females on the leaves of the plants after 24 h, the females dead or not on a leaf after 24 h and the percentage leaf surface of a certain leaf age class are given in Table 3. After 24 h we found 72% and 85% of the originally released females on the leaves of cv. 'Parade' and 'Fame', respectively. The distribution of females, after the first alightment, did not differ from the expected distribution based on the leaf area of the three leaf age classes for cv. 'Fame' (Chi-square test, $0.3 > P > 0.2$). First alightments of whiteflies can be qualified therefore as random. On cv. 'Parade' a significant different distribution than expected was observed (Chi-square test, $0.01 > P > 0.001$): a lower % than expected landed on young leaves and a higher % on old leaves. The distribution of the females and of the eggs after 24 h is significantly different from the expected distribution, based on the leaf area of the three leaf age classes (Chi-square test, $P << 0.001$ for both cultivars and statements).

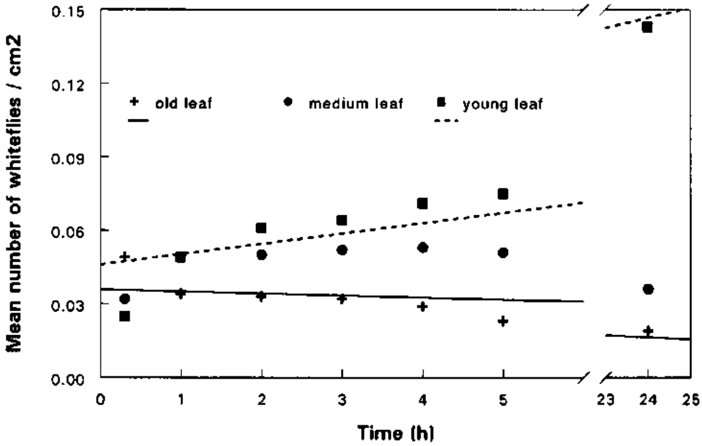

Figure 5. Dispersal of greenhouse whitefly females in a leaf age choice situation: mean number of whitefly females per cm^2 on leaves of three different age classes during a period of 24 h, *Gerbera* cv. 'Parade', leaves offered at the same level.

The young leaves have on both cultivars a much larger fraction of the whitefly population and of eggs, while the other leaf age classes have a lower fraction of females and of eggs than expected. An illustration of the dispersal process when leaves are offered on one level is given in Figure 5. The number of females per cm^2 changed on all three leaf ages during 24 h. The number increased on the young leaves and decreased on the old leaves. On the medium age leaf we see first a slight increase and eventually a decrease in number of females. Regression analyses gave a positive linear regression on the young leaves ($r^2 = 0.96$, $P = 0.0008$) and a trend towards a negative linear regression ($r^2 = 0.49$, $P = 0.08$) on the old leaves. The distribution of eggs among the leaf ages is not significantly different on both cultivars (Figure 6) (Mann-Whitney W test, P = 0.99). Most eggs are laid on the young leaves (Figure 6), even more than expected from the distribution of the females over the leaves (see Table 3). Only 20 to 30 % of the eggs are found on the medium and old leaves.

Table 3. The distribution of *Trialeurodes vaporariorum* females after first alightments on young, medium and old leaves (%) and the final distribution of the females after 24 h (%) on three leaf ages of *Gerbera* cultivars 'Fame' and 'Parade', leaves offered at one level.

	Cultivar		Leaf type	
		Young	Medium	Old
% Females (after 1st alightment)	'Fame'	30.8	40.2	29.0
	'Parade'	25.7	40.6	33.7
% Females (after 24 h)	'Fame'	56.3	33.3	10.4
	'Parade'	72.8	21.6	5.6
% Eggs on leaves	'Fame'	68.8	24.2	7.0
	'Parade'	79.8	15.3	4.8
% Leaf area	'Fame'	26.8	49.1	24.1
	'Parade'	36.0	43.2	20.8

Females on leaves after 24 h: cv. 'Fame': 84.7% (n=382) cv. 'Parade': 72.0% (n=324)

Females dead, not on leaves or lost after 24 h:

cv. 'Fame': 15.3% (n=69) cv. 'Parade': 28.0% (n=126)

Egg to adult development and mortality on different leaf ages

Results on two life-history parameters of the greenhouse whitefly, development duration and mortality, are presented in Figure 7 and Table 4. The 50%-point (or median) of the egg-to-adult development duration of the whiteflies is 22.8, 22.3 and 22.5 days for the young, the medium and the old leaves, respectively (Figure 7). The Kolmogorov-Smirnov test gives no significant differences when comparing the cumulative distributions of the duration of development on the different leaf ages. The only exception is the duration of development on medium and old leaves, which is caused by the tails of the curves (Figure 7). The total whitefly mortality is 43.5 % on the young leaves, which is lower than on both other leaf age classes (68 % and 67 % respectively, Table 4). The egg mortality is 20 - 25% on all three leaf ages.

Table 4. Egg mortality and total immature mortality of *Trialeurodes vaporariorum* on three leaf ages of *Gerbera* at 25 °C, cultivar 'Fame'.

Leaf type	Egg mortality (%)	Immature mortality (%)	Number of eggs
Young	19.2	43.5	209
Medium	24.8	68.2	214
Old	22.7	66.7	66

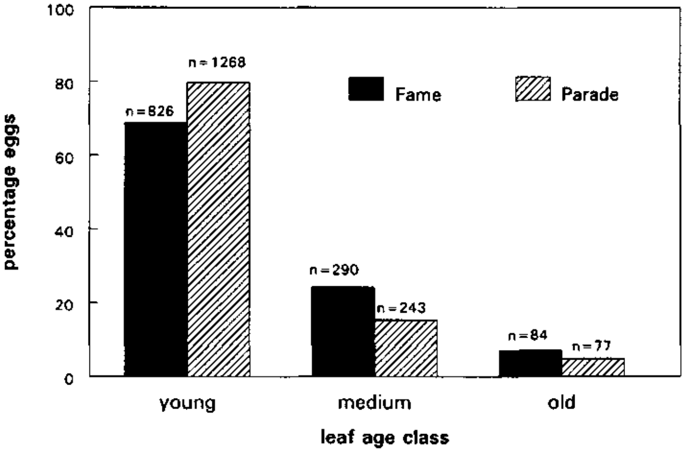

Figure 6. The egg distribution (%) of *Trialeurodes vaporariorum* on leaves of three different age classes of *Gerbera* after 24 hours. Total number (n) of eggs laid is given. *Gerbera* cultivars 'Fame' and 'Parade'.

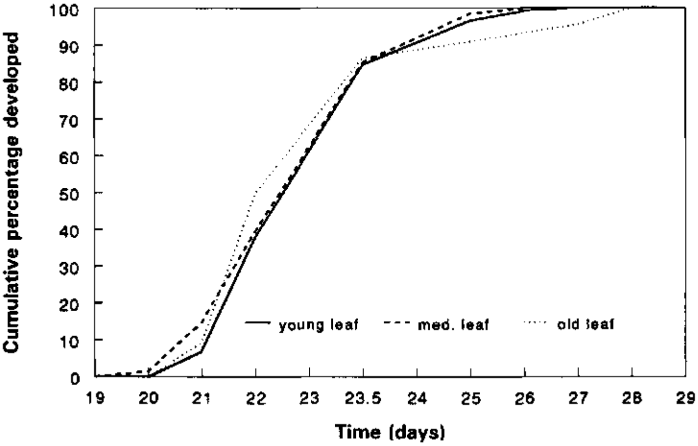

Figure 7. Development duration of *Trialeurodes vaporariorum* on leaves of three ages of the *Gerbera* cv. 'Fame' at 25 °C in a climate room.

DISCUSSION

The dispersal behaviour and distribution of the greenhouse whitefly on the host plants tomato and cucumber was studied by e.g. Eggenkamp-Rotteveel Mansveld et al. (1982 a, b), Noldus et al. (1985, 1986), Van Vianen et al. (1988) and Xu Rumei (1991). Movement of whiteflies started several hours after emergence, did not occur in the dark, and the rate of movement was found to be positively correlated with temperature (see also Ekbom, 1982). Part of the adults moved up vertically to the younger leaves within the same plant and at the same time another part of the population showed a horizontal and a vertical movement to neighbouring plants. Adult whiteflies, released in the centre of a *Gerbera* plant at stem level, aggregate after 24 h for 56 % (cv. 'Fame') to 73 % (cv. 'Parade') on the young leaves where they stay to feed and oviposit. In a more natural situation, when whiteflies emerged on a fullgrown *Gerbera* leaf of medium age, adult whiteflies fly after an average period of nine hours towards the centre of the rosette-plant. Thus, on *Gerbera*, the movement has an important horizontal component. The pre-flight period on the leaf of emergence fits the pre-oviposition period of one day of whiteflies reported for vegetable crops (see review Van Roermund & van Lenteren, 1992). The almost complete horizontal movement of the whiteflies on *Gerbera* is quite different from movements observed on vegetable crops (El Khidir, 1963; Ohnesorge et al., 1980; Noldus et al., 1985; Xu Rumei, 1991). The functional result is, however, similar: most adults alight and stay on the younger leaves. Final leaf choice is apparently not based on visual cues, but on probing behaviour of the whiteflies. This can be illustrated by the 'horizontal-level choice experiment', where we see that first landings occur at random on the three leaf age classes. On cv. 'Parade' less whiteflies than expected first alight on young leaves and more adults than expected alight on old leaves. During 24 h, old and medium leaves are gradually abandoned by the adult whiteflies. However, we do find adult females on all leaf types after 24 hours. When different leaf age classes are offered at the same horizontal level, 69 % (cv. 'Fame') to 80 % (cv. 'Parade') of the eggs are laid on the young leaf type. That is a larger percentage than expected from the proportional distribution of the adult females over the leaves in that situation (56 % and 73 %, respectively). The egg mortality is high on all three leaf age classes, 20 - 25%, when compared with the lower than 10% egg mortality generally found for whitefly on other host plants (see review van Roermund & van Lenteren, 1992).

We can conclude that adult *T. vaporariorum* females do prefer the young leaves for feeding and oviposition. Such an oviposition preference for young leaves has been shown for three citrus whitefly species on lemon (Walker & Zareh, 1990) and for *T. vaporariorum* on tomato (Noldus et al., 1985).

There may be at least two mechanisms determining the dispersal of insects that is directed to young leaves of a plant (Thompson, 1988). In the first place a feeding preference of the adults seems to be involved, which is related to the nutritional value of young leaves (Thompson, 1983; Noldus et al., 1985). Secondly, there is an obvious adaptive value to providing the sessile juvenile stages with food as long as possible on leaves that remain in a good condition during the developmental period of the sessile stages (Johnson, 1969; Ahmad, 1983). If feeding preference is hypothesized to have a biological meaning, it is necessary to measure the performance of insects on different leaf ages. The parameters we measured are developmental duration and mortality of whitefly stages. They were determined on three leaf age classes of cv. 'Fame' to detect a potential link between preference and performance of the greenhouse whitefly. Duration of development is not different on leaves of different ages, however, 23 % and 25 % more immature whiteflies die on the medium and old leaf ages compared to the young leaves. The performance, in terms of survival of whiteflies on different leaf types of a *Gerbera* plant, is thus linked to the preference of females for young leaves, which ultimately explains the movement and leaf selection behaviour.

Another characteristic that may affect oviposition and feeding by whitefly is the hairiness of the leaves. Price et al. (1980) discuss how pubescence may operate directly on herbivores. On leaves with a high trichome density or a leaf surface more covered by hairs, the relative humidity is higher, which may influence the life history and the behaviour of an insect. Also, the protection for a herbivore against its natural enemy might be better on hairy leaves. On hairy cotton, for example, *Bemisia tabaci* lays many more eggs and survival is better than on smooth cultivars, so adults and immatures are more abundant on pubescent cultivars (Butler & Henneberry, 1984; Butter & Vir, 1989). In our experiments, with intact plants where adults were released on the 'hairy' cv. 'Parade', 4.3 to 24.7 more adults were observed after 24 h on young leaves compared to medium and old leaves, while on the 'less hairy' cv. 'Fame' only 2.4 to 5.5 times as many adults were observed on the young leaf type. When whiteflies emerged on intact plants, they needed a significantly shorter period on the 'hairy' cv. 'Parade' before 50 % of the whiteflies had left the leaf of emergence. In addition, we found that females laid more eggs on the 'hairy' cv. 'Parade' (4.9 eggs/female) than on the 'less hairy' cv. 'Fame' (3.1 eggs/female) in the experiment where leaves were offered at the same horizontal level.

In conclusion, our study has shown that greenhouse whitefly:

-adults move after emergence to the youngest leaves in the heart of the rosette plant *Gerbera*,

-does show a preference for and has a higher performance on young *Gerbera* leaves compared with medium and old leaves, and

-seems to prefer hairy cultivars above less hairy ones for feeding and oviposition.

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CHAPTER 3

DISPERSAL AND DISTRIBUTION OF GREENHOUSE WHITEFLIES, *TRIALEURODES VAPORARIORUM* OVER A *GERBERA JAMESONII* CROP

SUBMITTED AS:
DISPERSAL AND DISTRIBUTION OF GREENHOUSE WHITEFLIES, *TRIALEURODES VAPORARIORUM* (HOMOPTERA: ALEYRODIDAE) OVER A *GERBERA JAMESONII* CROP
ENVIRONMENTAL ENTOMOLOGY

DISPERSAL AND DISTRIBUTION OF GREENHOUSE WHITEFLIES, *TRIALEURODES VAPORARIORUM* (HOMOPTERA: ALEYRODIDAE) OVER A *GERBERA JAMESONII* CROP

ABSTRACT

Dispersal and aggregation behaviour of the greenhouse whitefly, Trialeurodes vaporariorum (Homoptera: Aleyrodidae), were examined on the ornamental plant Gerbera jamesonii. In a set-up with a fixed number of host plants and releases of female whiteflies, we recorded the position of individuals during a period of five days in three experiments.

The whiteflies reached an average distance of 145 cm from the release point after five days. The average dispersal speed by a whitefly female was 20 cm/h during the first hours and dropped to 2-3 cm/h during the second and subsequent days. The observed spatial distributions of the whiteflies could be fitted to the negative binomial distribution in most cases. Whitefly populations were overdispersed, so strongly aggregated. Aggregation was density-dependent: aggregation increased with increasing whitefly density per plant. The results are discussed with respect to whitefliy distributions on other host plants and in relation to potential consequences for biological control of the greenhouse whitefly on Gerbera.

INTRODUCTION

The interaction of the polyphagous herbivore *Trialeurodes vaporariorum* (greenhouse whitefly) with host plants and its parasitoid *Encarsia formosa* has been studied extensively on vegetables (e.g., Van Lenteren & Noldus, 1990, Noldus & van Lenteren, 1990, Van Lenteren et al., 1995, Van Lenteren & Van Roermund, 1999), leading to reliable commercial biological control methods on major vegetable crops (Van Lenteren & Woets, 1988, Van Lenteren, 1995). However, *Trialeurodes vaporariorum* is a prominent pest insect in ornamental crops too. Different reasons, such as pesticide resistance, increasing costs of pesticides and governmental restrictions concerning extensive pesticide use, lead to incentives for other than chemical control of insect pests in ornamental crops both in the Netherlands and worldwide (e.g., Van Lenteren, 1990, Ravensberg & Altena, 1993, Albajes et al., 1999). To develop a robust biological control method of the greenhouse whitefly in ornamentals, it is essential to know the relationships between the host plant, the herbivorous insect and the parasitoid (e.g., Price et al., 1980). Part of this information concerns the spatial relationships of the herbivore in a crop.

In this paper, dispersal behaviour of *T. vaporariorum* over a *Gerbera jamesonii* crop is described. On a single *Gerbera* plant, the dispersal process of whiteflies leads to adult and egg aggregation on young leaves. One day after whitefly release the dispersal process ceased within a plant, and about 70 % of the adults and 80 % of the eggs are found on the young leaves. The conclusions hold for hairy and non-hairy *Gerbera* cultivars (Sütterlin & Van Lenteren, submitted). The aggregation of adults and eggs on young leaves through the dispersal behaviour of adults is similar to that found on vegetable plants like tomato and cucumber (Eggenkamp-Rotteveel Mansveld et al., 1982a,b, Ekbom, 1980, Martin et al., 1991, Noldus et al., 1985, Van Vianen et al., 1988 and Xu Rumei, 1991).

In tomato 90 % of the adults move upwards and the majority eventually settles in the top of neighbouring plants (Noldus et al., 1986). We expected that the rosette type of plant architecture of *Gerbera* might influence the dispersal behaviour of whitefly adults between plants, and thus the distribution of *T. vaporariorum* over a crop. Of particular interested was whether whitefly adults leave the canopy of *Gerbera* plants quicker, and disperse over a larger area than in a vertically-structured vegetable crop. If they would show the same behaviour as on tomato and cucumber, i.e. a strong vertical movement, one would expect that they even depart entirely from the rosette plant on which they emerged and redistribute over the crop. The end result would then either an apparent random or a regular distribution pattern over a *Gerbera* crop.

Taylor et al. (1978), however, state that spatial randomness is highly improbable in the distribution patterns of living organisms. In a review of the spatial distribution of herbivorous insects, Stanton (1983) distinguishes two groups of factors generating non-random herbivore distributions: (1) the increased success of herbivores by either decreased starvation or dispersal risk, by buffered microclimate or by the host plant quality, and (2) the increased number of herbivore colonists via high herbivore immigration or low emigration. In addition to observing behaviour, an approach to gain insight in the pattern of movement of whiteflies is to describe the distribution of the insects mathematically.

In order to determine in what manner and how quickly the plant to plant movement takes place, and on which plants whiteflies remain, we used an experimental crop situation with *Gerbera* plants where we released *T. vaporariorum* females. We followed the dispersal of whiteflies between plants to be able to analyse the migration behaviour in a *Gerbera* crop.

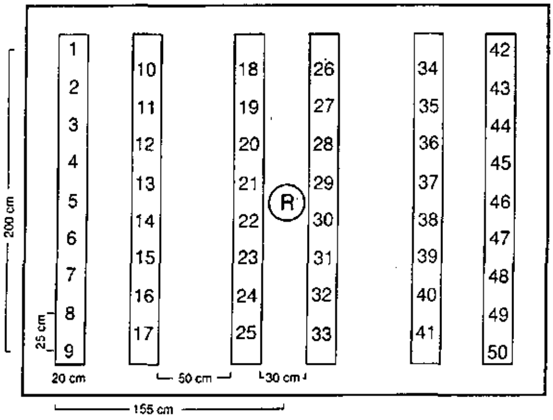
MATERIALS AND METHODS

Experimental procedure

Fifty plants of the *Gerbera* cultivar 'Fame' was used for this experiment. In a glasshouse of 15 m2, 50 plants were placed in three 'double' rows on benches. Four middle rows had eight plants each and both edge rows consisted of nine plants. The plants were 25 cm apart from each other in the same row and 30 cm across the same double row. The distance between the benches was 80 cm. During the experimental period of 3 weeks, the plants had about eight fully grown leaves. The leaves were classified into three age groups: (i) young leaves, (ii) medium leaves, and (iii) old leaves as described in Sütterlin & van Lenteren (submitted). In the centre of the glasshouse, 500 adult female whiteflies were released from five glass vials (Figure 1). The whitefly adults were collected randomly from the young leaves of a rearing kept on *Gerbera*, cv. 'Fame'. Every hour, from 8.30 a.m. until 6.30 p.m., the position of the females on the leaves of every plant was checked carefully by sight with a hand mirror, and recorded. After five days, the adults were removed. The same procedure was followed in a second experiment.

Whiteflies do not move in dark (Sütterlin & van Lenteren, submitted), but movement is possible during the whole daylight period. Therefore, in a third experiment, the position of females was recorded from sunrise (6.30 a.m.) to sunset (10.00 p.m.) during five days. The experiments were carried out for three consecutive weeks (week numbers 26, 27 and 28). The natural photoperiod (sunlight) was used, and mean temperatures (±*SD*) were 25.5 ±6 °C, 25.8 ±5 °C and 24.8 ±5 °C, respectively, during the three weeks. The mean relative humidity (±*SD*) was 60.9 ±13%, 56.3 ±11% and 41.6 ±8%, respectively.

In this paper, data from the third experiment will be presented mainly, because here whitefly movement was recorded during the whole of the potential flight period from sunrise to sunset. To compare the different populations, specific results from the other two experiments are presented also.



all numbers represent gerbera plants

Ⓡ =release point; 5 glassvials, each containing 100 ♀♀

Figure 1. Set-up of dispersal experiment of *Trialeurodes vaporariorum* females on *Gerbera* plants, cultivar 'Fame' in a glasshouse.

Statistical methods

To assess how whitefly populations are aggregated in the crop in the course of time, the maximum likelihood estimate of the parameter k of the negative binomial distribution was computed (see Table 2) according to the method of Bliss & Fisher (1953). After fitting the theoretical distribution to the data, the goodness of fit was tested using chi-square analysis. The parameter k is supposed to be consistent at all densities (Taylor et al., 1978). The relationship of the degree of clumping (1/k) (Bliss, 1971) and the whitefly density (m) was examined by regressing 1/k on m. The shape of the curve was compared with the four types discussed by Taylor et al. (1979).

The distribution of the whiteflies was analysed further using crowding and aggregation parameters: the mean crowding index (m^*) of Lloyd (1967) and the variance-mean ratio of Taylor (1984) at different time steps. If $m^*/m > 1$, the whitefly distribution is aggregated and overdispersed (i.e. a clustered occurrence of insects). Taylor's power law (variance = a. mean^b) was used to demonstrate wether density-dependence of aggregation occurred (Taylor et al., 1978). In that case, the log of the variance has to increase linearly with the log of the mean at a rate >1.

RESULTS

In the three experiments, the pattern of movement of whitefly females among the 50 plants was similar. Only data from the third experiment are shown in Figure 2. Shortly after release from the glass vial, the whitefly females alight and stay on plants near the release point. High peaks occur in number of individuals on the plant numbers 21, 22, 29 and 30, i.e. on plants 20 - 30 cm from the release point. Crossings from plants of the the central double row to plants of the neighbouring double rows were scarcely observed during the first day. Some whiteflies reached three of the 'corner' plants in the glasshouse at a distance of 184 cm from the release point during the second day (Figure 2, day 1). Movement in all directions was observed, and most plants were visited by at least one female by the third day after release (Figure 2, day 3). Some plants, always situated near the release point in the central double row, held more than 30 whiteflies. The net result of movement of the whiteflies during the third day was virtually nil. A relatively stable distribution of females was found on day four and day five of the experiment (Figure 2, day 4 and 5).

Whitefly movement is expressed as the average distance all females have travelled from the release point during a certain period of time. The average distance moved increased linearly during the whole experiment (α = 0.01, $P < 0.001$). On the third day the whiteflies were on average about 105 cm from the release point. The distance increased somewhat on day four and five to 145 cm (Figure 3). The average whitefly dispersal speed decreased from above 20 cm/h during the first five hours on day 1 of the experiment to around 3 cm/h on consecutive days (Table 1).

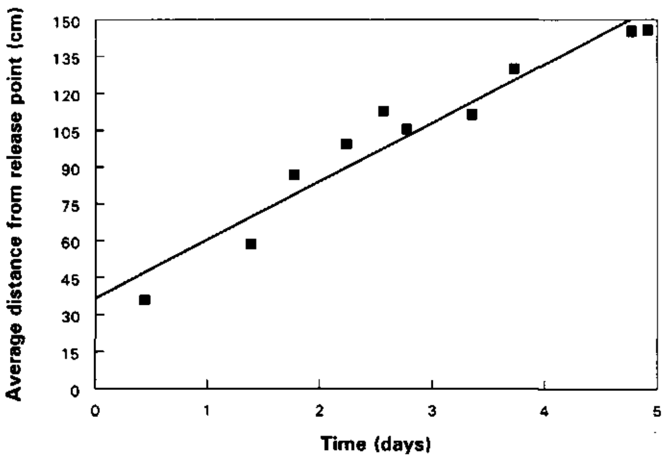


Figure 3. Average distance moved of a *Trialeurodes vaporariorum* population from the release point in a *Gerbera* crop during five days (Experiment 3). Linear regression is significant, $P < 0.001$.

$y = 36.71 + 23.79\,x$; $r^2 = 0.93$

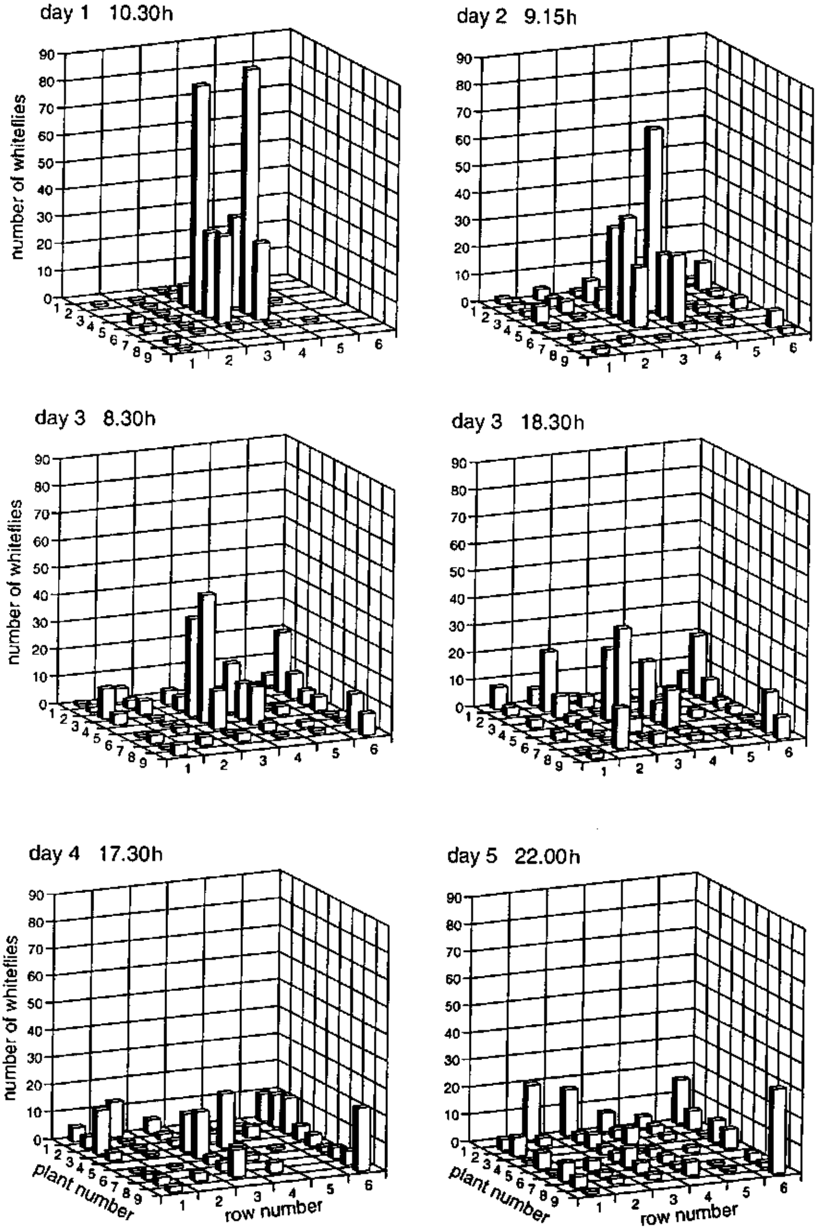


Figure 2. Distribution of whitefly females at various time intervals during a five day period over *Gerbera* plants in a glasshouse (Experiment 3).

Table 1. Average dispersal speed of *Trialeurodes vaporariorum* females on *Gerbera* plants, cv. 'Fame', during the daylight period of five consecutive days (Experiment 3).

Day	Time (h:m)	Dispersal speed (cm/h)
1	10:30	23.94
2	9:15	3.72
2	18:15	3.37
3	8:30	3.26
3	13:30	3.01
3	18:30	2.61
4	8:30	2.27
4	17.30	2.36
5	18:30	2.03
5	22:00	1.95

The actual distributions of whitefly females over the plants were compared with the negative binomial distribution (Table 2). In many cases a good fit of the theoretical distribution to the experimental data was found. The whiteflies seem to be even stronger aggregated in six cases, where a significant difference between the experimental data and the negative binomial distribution was found (Table 2). Values for parameter k are also given in Table 2. However, the distributions could not be fitted by a common k, which means that the distributions cannot be characterized by one simple parameter. The degree of clumping (1/k) increased with the whitefly density per host plant in experiment 3 (Figure 4).

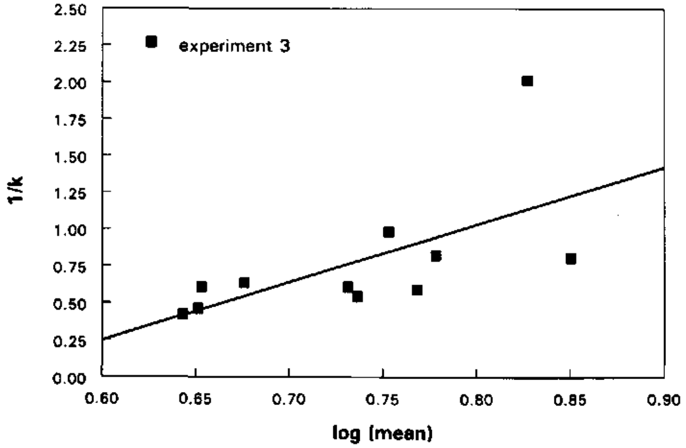


Figure 4. Relationship between the degree of clumping (1/k) and the mean number of *Trialeurodes vaporariorum* females per *Gerbera* plant (Experiment 3). Linear regression is significant, P = 0.0387.

$y = -2.09 + 3.91\,x$; $r2 = 0.39$

The mean crowding index m*, representing the mean number of other individuals per individual in a unit of space (Lloyd, 1967), was around 100 at the start of the three experiments. It decreased eventually to 6, 2 and 11 in experiments 1, 2 and 3, respectively. Also the variance-mean ratio of Taylor decreased from about 100 to less than 10 in all three experiments (Table 3). Mean crowding indices and the variance-mean ratios did not differ significantly among all three experiments (Kruskal-Wallis test, α = 0.05, P = 0.255). Although both parameters decreased, the adult whitefly populations stayed aggregated during the whole observation period in all three experiments: m*/m > 1 (Figure 5).

For the parameter m*/m, the three experiments did not differ significantly (Kruskal-Wallis, α = 0.05, P = 0.534). A very high degree of aggregation was found after releasing the adults (m*/m ratio of 13). After three and a half days the distribution of whiteflies stabilized and remained similar until the end of the experiments. The relation between the degree of aggregation and time (or age of the whitefly females) can be described by a significant exponential decreases (P = 0.005 and r^2 = 0.75; P = 0.001 and r^2 = 0.72; P = 0.004 and r^2 = 0.78 for Experiments 1, 2 and 3, respectively). The curves decreased over time until the m*/m values were between 2 and 2.5 (Figure 5).

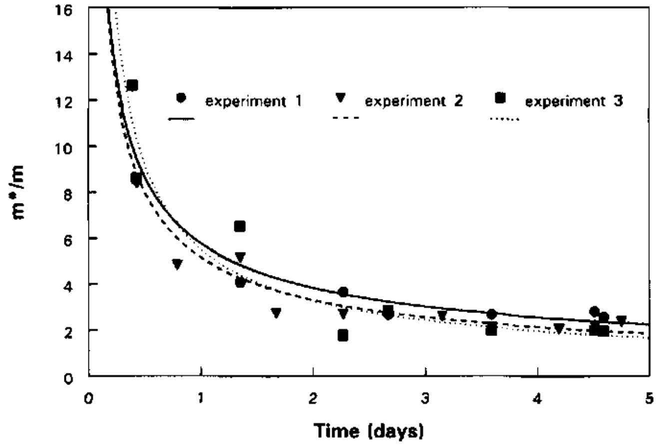


Figure 5. Degree of aggregation or patchiness (after Lloyd, 1967) of three whitefly populations in a *Gerbera* glasshouse during a five day period. Exponential regressions were significant, P = 0.005; P= 0.001; P = 0.004 for Experiments 1, 2 and 3, respectively.

Experiment 1: $y = 10 \exp(2.19 - 0.31 x)$; $r^2 = 0.75$

Experiment 2: $y = 10 \exp(2.04 - 0.32 x)$; $r^2 = 0.72$

Experiment 3: $y = 10 \exp(2.30 - 0.41 x)$; $r^2 = 0.78$

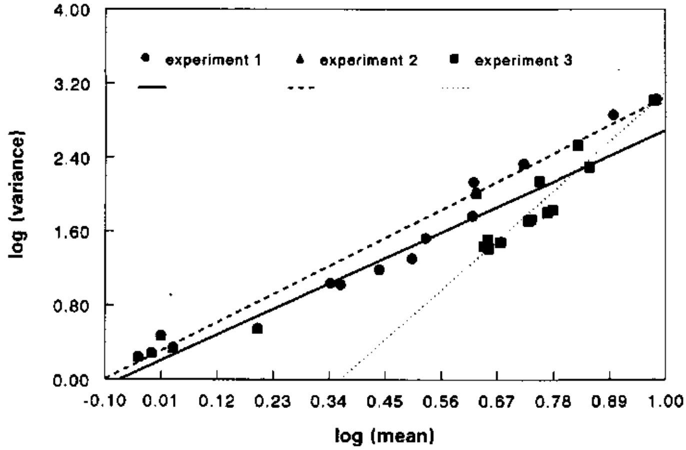


Figure 6. Relationship between mean and variance of three populations of *Trialeurodes vaporariorum* females on *Gerbera* plants, cv. 'Fame'. Linear regressions were significant, $P < 0.001$; $P = 0.002$; $P < 0.001$ for Experiments 1, 2 and 3, respectively.

Experiment 1: $y = -0.26 + 3.47\, x$; $r^2 = 0.96$

Experiment 2: $y = 0.44 + 2.70\, x$; $r^2 = 0.81$

Experiment 3: $y = -1.76 + 4.87\, x$; $r^2 = 0.91$

The density dependence of aggregation is illustrated in Figure 6. The log of the variance increased linearly with the log of the mean in all three experiments ($a = 0.001$; $P_1 < 0.001$; $P_2 = 0.002$; $P_3 < 0.001$). The r^2-values of the regressions are 0.98, 0.81 and 0.91 for Experiments 1, 2 and 3, respectively. Parameters *a* and *b* of Taylor's power law are in the first experiment 1.121 and 3.177, in the second experiment 0.437 and 2.244, in the third experiment 1.853 and 3.184, respectively. The parameter *b* is significantly different from 1 in all experiments (*t-test*, $P < 0.001$).

Table 2. Parameter k of the negative binominal distribution of whitefly populations on *Gerbera* at various times during three experiments and the chi^2-values of the differences between the observed frequency distributions and the expected ones under the theoretical negative binominal distribution (df = degrees of freedom; n.s. = not significant, ($\alpha = 0.05$).

Time (day, h:m)	*k*	chi^2-value	df	significance
Experiment 1				
day 1, 10:50	0.2457	1.550	1	n.s.
day 2, 9:30	0.8421	8.092	3	$0.02 < P < 0.05$
day 3, 8:30	0.6101	0.217	3	n.s.
day 3, 18:30	1.1733	2.885	3	n.s.
day 4, 17:30	0.7952	2.165	3	n.s.
day 5, 16:30	0.6436	1.724	2	n.s.
day 5, 18:30	0.9309	1.633	3	n.s.
Experiment 2				
day 1, 10:30	0.4476	5.045	2	$0.02 < P < 0.05$
day 2, 9:30	0.8655	4.138	3	n.s.
day 3, 8:30	1.2509	0.526	2	n.s.
day 3, 18:30	0.5439	1.120	1	n.s.
day 4, 17:30	1.0390	0.864	1	n.s.
day 5, 16:30	1.4294	0.221	1	n.s.
day 5, 18:30	1.2187	0.010	1	n.s.
Experiment 3				
day 1, 10:30	0.4967	5.196	2	$0.05 < P < 0.1$
day 1, 19:30	1.2438	6.867	4	n.s.
day 2, 9:15	1.0160 1	3.080	4	$0.01 < P < 0.02$
day 2, 17:15	1.2160	3.331	4	n.s.
day 3, 8:30	1.6950 1	1.151	5	$0.02 < P < 0.05$
day 3, 14:30	1.4971 1	2.297	5	$0.02 < P < 0.05$
day 3, 18:30	1.8426	5.090	5	n.s.
day 4, 6:30	1.6469	5.987	6	n.s.
day 4, 16:30	1.6973	8.915	5	n.s.
day 4, 17:30	1.5723	8.116	4	n.s.
day 5, 16:30	2.3771	3.558	5	n.s.
day 5, 18:30	1.8113	3.502	5	n.s.
day 5, 22:00	2.1650	3.467	5	n.s.

Table 3. Mean number of adult whitefly females per plant at several time intervals, mean crowding (m* after Lloyd, 1967) of females, and variance-mean ratio (after Taylor, 1984) at three experiments on *Gerbera*, cv. 'Fame'.

Day	Time (h:m)	Number of adults	m	s^2	m*1)	s^2/m1)
Experiment 1						
1	9:50	394	7.88	728.68	99.35	92.47
1	10:50	210	4.20	136.90	35.80	32.60
2	9:30	209	4.18	58.35	17.14	13.96
3	8:30	169	3.38	33.84	12.39	10.01
3	18:30	159	3.18	20.31	8.57	6.39
4	17:30	137	2.74	15.38	7.35	5.61
5	16:30	110	2.20	10.94	6.17	4.97
5	18:30	115	2.30	10.58	5.90	4.60
Experiment 2						
1	9:30	479	9.58	1076.97	121.0	112.4
1	10:30	263	5.26	216.11	45.35	41.09
2	9:30	213	4.26	104.77	27.85	24.59
3	8:30	79	1.58	3.55	2.83	2.25
3	18:30	51	1.02	2.96	2.92	2.90
4	17:30	46	0.92	1.75	1.82	1.90
5	16:30	49	0.98	1.94	1.96	1.98
5	18:30	54	1.08	2.20	2.11	2.04
Experiment 3						
1	9:30	474	9.48	1054.62	119.73	111.25
1	10:30	336	6.72	340.70	56.42	50.70
1	19:30	354	7.08	199.38	34.24	28.16
2	9:15	302	5.66	139.20	29.25	24.59
2	17:15	300	6.00	68.41	16.40	11.40
3	8:30	293	5.86	64.33	15.84	10.98
3	18:30	272	5.44	53.92	14.35	9.91
4	17:30	237	4.74	30.40	10.15	6.41
5	8:30	225	4.50	26.17	9.32	5.82
5	22:00	224	4.48	32.21	10.67	7.19

m = mean number per plant; s^2 = variance; s^2/m = variance-mean ratio

1) No significant difference was found between the mean crowding m* and the variance-mean ratio s^2/m in the three experiments (Kruskal-Wallis, $\alpha = 0.05$, P = 0.255).

DISCUSSION

Amongst *Gerbera* plants an aggregated spatial distribution of *T. vaporariorum* was found during the whole observation period of five days. This pattern appears to be typical for this species, and is also found on tomato and cucumber plants (Ekbom, 1980; Ekbom, 1982; Noldus et al., 1986; Xu Rumei, 1991). The level of aggregation of whitefly females on *Gerbera* stabilized after three and a half days, and remained overdispersed. This was also found for tomato plants (Noldus et al., 1986). The average distance travelled by whiteflies during three and a half days is about 105 cm from the release point, and the dispersal speed is then approximately 3 cm per hour. Again, this was also reported for tomato (Noldus et al., 1986; van Vianen et al., 1988). Yet, a distinct equilibrium point like in the experiment of Noldus et al. (1986) was not reached. On the fifth day the females were found on average 145 cm from the release point and the dispersal speed had dropped to 2 cm/h. Dispersal patterns of whitefly populations described by van Vianen et al. (1988) show a same increase in average distance travelled after an initial equilibrium point had been reached. Because of the similarity in results for tomato and *Gerbera*, the influence of the host-plant architecture of *Gerbera* on the dispersal and final distribution of *T. vaporariorum* in a crop seems to be small.

The negative binomial distribution has been shown to fit a remarkable variety of population counts (Bliss, 1971), and also the data described here agree with this distribution. In parasitoid - host relationships the degree of clumping (sensu Bliss, 1971), is often assumed to be density-independent (Anderson & May, 1978). Alternatively, it is found to decrease with parasitoid density (Zhang et al., 1993), which is supposed to be due to increased parasitoid-induced mortality of hosts. The degree of clumping has been studied rarely in herbivore - host plant interactions. Asante et al. (1993) reported that they could not find a significant relationship between the reciprocal of k and the mean density of wooly apple aphid, *Eriosoma lanigerum*, in an apple orchard. The degree of clumping of *T. vaporariorum* on *Gerbera* plants does increase with the insect density. This also indicates why a common k for the whiteflies 'in all parts of their density range' (Taylor et al., 1979) could not be found. It justifies the use of other methods and parameters for defining aggregation in a distribution. Whether the response curve of the regression of the degree of clumping $(1/k)$ on log m follows Taylor's type IV curve ($3 < b$ then $1/k \rightarrow \infty$ as $\mu \rightarrow \infty$ with ever-increasing positive slope, Taylor et al. (1979)) is difficult to say. In the work described here, measurements were only made over a limited density range.

Taylor (1984) states that although the negative binomial distribution often fits biological data, is 'not useful in describing dispersal over time and a range of densities'. Fitting data to theoretical distributions gives only qualitative results. It is more meaningful to plot aggregation indices against time (Xu, 1991), as is done in our Figure 5 and Table 3. After the second day, the mean crowding, m^* of adult greenhouse whiteflies on *Gerbera* is in our experiment the same as reported for the third instar larvae of cinnabar moths in the field (van der Meijden, 1976). The m^*/m index of aggregation is comparable to the ones reported for five greenhouse whitefly populations on cucumber and tomato by Ekbom (1980).

Although we could clearly demonstrate density dependence of aggregation, a sinlge common relationship between whitefly density and aggregation on *Gerbera* could not be established. Whitefly populations of the same species are expected to behave the same on one *Gerbera* cultivar. Burla & Bächli (1993) report a common relationship between density and aggregation for two *Drosophila* species on Cornelian cherries in the field. The spatial behaviour of the whiteflies might have been different between our experiments because of external factors like temperature and relative humidity. During our second experiment, many whiteflies died after the second day which may have been caused by high peak temperatures in that week. The slopes of the linear regressions between density and aggegation are above 1 in all experiments and higher than reported for the two *Drosophila* species (Burla & Bächli, 1993). Taylor et al. (1978) give values between 1.36 and 1.91 for two aphid genera, *Myzus* and *Aphis* on beans and plums. For the greenhouse whitefly Xu (1991) reports a value of 2.21 in the field, although the host plant is not mentioned. On *Gerbera* higher values are found for the slopes of the linear regressions, so the populations are more strongly aggregated in the greenhouse.

Aggregation and its density dependence have been described for many other herbivores: Chrysomelidae (Bach & Carr, 1990), Scolytidae (Birch, 1984), Mexican bean beetle (Coccinelidae) (Turchin, 1987), cinnabar moth (Arctiidae) (van der Meijden, 1976) and for insect parasites (Zhang et al., 1993). Among the explaining hypotheses are mating purposes and better survivership in larger groups by either increased foraging efficiency or a lower predation rate (Southwood, 1962; Stanton, 1983). In addition, Bach & Carr (1990) mention resource quality differences between plants as an explanation for aggregation on particular plants. Some evidence for this is provided for *Tyria jacobaeae* on *Senecio jacobaea* by van der Meijden (1976). In herbivorous insects this certainly deserves further attention. We worked with the *Gerbera* cultivar 'Fame' and plants were produced from a meristem culture, so differences between these clones were expected to be small. However, differences in nutrient and water uptake may still lead to qualitative differences between plants.

An increasing degree of clumping with increased herbivore density on the host plants means that only a few plants will be overexploited through foraging by whiteflies. An extremely aggregated distribution could lead to interference between herbivores. On glasshouse vegetables Xu (1983) found a decrease in oviposition frequency at densities above 4 adults per cm^2, while Yano (1988) reported no significant decrease in oviposition frequency at densities up to 10 adults per cm^2. The whitefly density in our experiments never exceeded 0.05 adult per cm^2 (80 adults per plant), so interference effects are not expected here.

Whitefly aggregation may influence the search behaviour of parasitoids and, thus, success of biological control (van Lenteren & van Roermund, 1999). The spatial distribution of *T. vaporariorum* over *Gerbera* plants resembles the distributions between vegetable host plants like cucumber and tomato. Aggregation of whiteflies in tomato crops did not hamper the parasitoid *E. formosa* to effectively find its hosts and reduce the whitefly numbers to far below the Economic Injury Level (Van Lenteren & Woets, 1988). Based on the results for *Gerbera* reported in this paper, it is not expected that the whitefly distribution pattern negatively influences the possibilities for biological control on this ornamental crop.

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CHAPTER 4

INFLUENCE OF HAIRINESS OF *GERBERA JAMESONII* LEAVES ON THE SEARCHING EFFICIENCY OF THE PARASITOID *ENCARSIA FORMOSA*

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INFLUENCE OF HAIRINESS OF GERBERA JAMESONII LEAVES ON THE SEARCHING EFFICIENCY OF THE PARASITOID ENCARSIA FORMOSA

ABSTRACT

To characterize the relationship between the leaf surface of ten *Gerbera jamesonii* Hooker cultivars and the searching behaviour of the parasitoid *Encarsia formosa* Gahan on a leaf, the trichome density and shape were described. Both parameters varied largely among the cultivars. The density varied from 80 to more than 1000 trichomes per cm^2 and the hair shape from single erect trichomes to tapestries of entangled trichomes above the leaf surface. The walking activity, speed and pattern were the tested parameters of the parasitoid searching behaviour on the leaf. In spite of the differences in leaf surface structure the walking activity was around 75 % on most cultivars. The walking speed was between 0.2 and 0.3 mm/s on all cultivars and was not significantly different from the speed on tomato. That hairiness in general does hamper the parasitoid females was illustrated by the walking speed on the hairless sweet pepper (0.73 mm/s). On all tested cultivars, a rise of temperature of 5 °C gave the same significantly higher walking speed (0.39 mm/s) of *E. formosa* females. The relative straightness of the walking track was high and the same on all cultivars. Consequences of the results of the searching behaviour of *E. formosa* on *G. jamesonii* cultivars are discussed with respect to other host plants and other parasitoids. As walking speeds are the same on *Gerbera* and tomato, and reproduction is also similar on these two host plants of the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood), we conclude that biological control of whiteflies on *G. jamesonii* is a realistic option.

INTRODUCTION

Biological control of the greenhouse whitefly *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae) with the parasitoid *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) has been applied on glasshouse vegetables since the 1920s. Data on the use of *E. formosa* can be found in van Lenteren & Woets (1988) and reviews on the research of the tritrophic relationship between plant, pest and natural enemy are given by van Lenteren & Noldus (1990), Noldus & van Lenteren (1990) and van Lenteren et al. (1996). At present, the use of biological pest control as the cornerstone of IPM programmes is strongly stimulated by governmental policies. For greenhouse vegetables such programmes are now commonly used (van Lenteren, 1995) and the development of such programmes for ornamental crops are of high priority (Fransen, 1992).

Basic knowledge on biology and behaviour is needed to understand and possibly improve a tritrophic relationship between the greenhouse whitefly, the parasitoid *E. formosa* and an ornamental host plant (Sütterlin & van Lenteren, submitted). *Gerbera jamesonii* seems to be a good ornamental host plant to start with, because only the flowers are marketed and a certain degree of injury or even whiteflies present on the leaves can be tolerated. This does not lead to a reduction in quality or price of the flowers. In *Gerbera* crops whitefly species are the main pest insects. The *G. jamesonii* host plant suitability for greenhouse whitefly resembles that of the vegetable tomato (van de Merendonk & van Lenteren, 1978; Dorsman & van de Vrie, 1987), a crop in which the greenhouse whitefly is controlled very effectively by *E. formosa*. A wide range of *G. jamesonii* cultivars are grown. Cultivars may vary substantially in leaf size and in leaf surface structure (van Lenteren & de Ponti, 1990). Two characteristics of leaf surface structure, the wax layer and the plant hairiness, can influence parasitoid behaviour. For example, wax layers can adsorb and re-release insect sex pheromones (Colwell et al., 1978). However, little is known on the functional differentiation of epicuticular waxes relevant to insect-plant relationships (Jeffree, 1986). Trichome diversity in plants is well known and the function of plant hairs is manifold: (i) climbing, (ii) shedding water, (iii) preventing desiccation and reducing transpiration, (iv) providing optical qualities and (v) hampering and trapping insects (Jeffree, 1986). Also, the microclimate (e.g. temperature, relative humidity and wind speed) on the leaf surface is affected by hair type and density. Insects may profit as well as being hampered from the conditions on the surface (Southwood, 1986).

The leaf hairiness may influence the walking behaviour of *E. formosa*. Walking of a parasitoid consists of its (i) walking activity, (ii) walking speed and (iii) walking pattern. The walking activity is the time a parasitoid is walking on a leaf, as a percentage of the total time spent on that leaf surface, excluding handling of a host. This activity determines the actual time the parasitoid moves and can possibly encounter hosts. The searching behaviour of *E. formosa* is random, therefore the encounter rate with hosts strongly depends on the walking speed of the parasitoids (van Lenteren et al., 1976) and the walking pattern. In a cucumber cultivar with a hair density half that of traditional cultivars, the parasitoid's walking speed increased from 0.20 mm/s to almost 0.40 mm/s (van Lenteren et al., 1995). It is, therefore, hypothesized that the walking speed of *E. formosa* is highly influenced by plant species or cultivars with differences in the leaf surface. The walking pattern or sinuosity of the track of *E. formosa* is the third determining factor of movement. The searched area is largest, when the sinuosity of a track is low. In other words: the walking path should be a 'straight' ongoing movement (Bell, 1991). Recrossing of a path does seldomly occur then. When the path is more winding, the effectiveness of searching 'unknown' territory decreases, because already 'known' territory is visited again. A 'random searcher' should therefore choose a straight walking path to find its (first) host. To remain in the same small area can be a strategy for a parasitoid or predator after encountering the first host or prey or a chemical substance that indicates the presence of hosts (e.g. contact chemical). This strategy leads to more encounters, if hosts/prey are aggregated. Arrestment effects and increased turning rates in the presence of host honey dew are found in *Eretmocerus* and *Encarsia* species (Shimron et al., 1992 and van Vianen & van de Veire, 1988) and also in carabid beetles, once they have reached their prey in the field (Mols, 1993).

If *Gerbera* leaf hairiness has an important negative effect on either walking activity (less walking), walking speed (slowing down) or walking pattern (less straightness), it would result in a lower encounter rate of *E. formosa* with its hosts. This affects the biological control of *T. vaporariorum*. Before testing *E. formosa* as a biological control agent at the glasshouse level in *G. jamesonii* crops, the influence of different leaf surfaces on the parasitoid behaviour was investigated.

The trichome density and hair shape of 10 *Gerbera* cultivars is described in this paper, to characterize the relationship between the plant (leaf) surface of the ornamental plant *G. jamesonii* and the searching behaviour of the parasitoid *E. formosa*. The walking activity, speed and pattern, as important parameters of the searching behaviour of the parasitoid, have been analysed on the different cultivars and leaf surfaces. Temperature is another parameter that may influence the walking speed of *E. formosa* (van Roermund & van Lenteren, 1995). So, different growing conditions of crops can influence the efficiency of the parasitoid as well. The walking speed of *E. formosa* is determined on several cultivars in a temperature range from 20 to 30 °C.

MATERIAL AND METHODS

Plant material.

The *G. jamesonii* cultivars 'Dragon', 'Estelle', 'Fame', 'Irmgard', 'Macho', 'Pacific', 'Parade', 'Party', 'Provence' and 'Tennessee' were used for measuring trichome density and shape. The plants were grown in a glasshouse compartment at a mean temperature of 20 ± 1°C and a light regime of 16L:8D. *Gerbera* plants had eight full grown leaves and were three to four months old when used in the experiments.

Leaf hair density and length.

The hair density was determined by counting the number of trichomes on the underside of leaf discs with a diameter of 5 mm under a binocular microscope, at a magnitude of x10. For the cultivar 'Fame' we analysed 50 leaf discs (from the base, centre, edge and top of the leaves) of full grown leaves (leaf numbers four and five, counted from the youngest unfolded leaf of the rosette) from five different plants. For each of the nine other cultivars 10 leaf discs per plant from two different plants were analysed. Differences between the cultivars were tested with a Kruskal-Wallis test (α = 0.05) followed by a multiple comparison test. The length of the trichomes was measured on 10 leaf discs (10 hairs per disc) for every cultivar. Differences in trichome length between cultivars were statistically tested in the above mentioned way.

Plant hair shape

Leaf surfaces of the Gerbera cultivars were studied with a scanning-electron-microscope (SEM). For preparation of the plant material (fixation, drying and sputtering of an argon layer on the material) we refer to the procedure given in Nagl (1981). Photographes of the leaf surface were taken with a magnitude of 50 to 350 times. A classification of hairs was made according to those SEM-photographs and after studying the trichomes with a binocular microscope.

Parasitoids

Black pupae were obtained weekly on cards from 'Koppert Biological Systems'. Cards were placed in glass petri dishes of 5 cm diameter. The parasitoids that emerged were provided with a droplet of honey placed on the petri dish. Naive (without earlier host contacts) *E. formosa* females, not older than 16 hours were used in the experiments. The females were kept at a temperature of 20, 25 or 30 °C, in anticipation of the experimental conditions.

Walking activity

The walking activity, speed and pattern of the parasitoid *E. formosa* was determined on eight of the above mentioned *Gerbera* cultivars. Cv. 'Pacific' and 'Provence' were not used. To get an impression of the wasps' walking activity during searching bouts it is necessary to record behavioural elements. During the video recordings, described in the section 'walking speed', three behavioural elements of *E. formosa* were recorded on a portable computer; walking, standing still and jumping. At the same time the wasp's location was recorded. The walking activity of a female was defined as the percentage time walking out of the total time spent on the leaf. The walking behaviour was recorded for a maximum of five minutes. If *E. formosa,* however, stood still for more than two minutes or walked on the perspex ring or the petri dish lid longer than one minute, the recording was stopped. Between 11 and 25 females per *Gerbera* cultivar were tested.

Whether a relationship exists between walking activity and walking speed was investigated in the following way. All wasps with a walking activity of less than 50 percent were checked for their individual walking speed. A sign (plus or minus) was given per wasp to indicate wether this individual's speed was higher or lower than the mean walking speed of females on that cultivar. Significantly more negative signs would reveal a correlation between a low walking activity of up to 50 percent and a low walking speed on that cultivar.

Walking speed

For a comparison of the walking speed with the behaviour of *E. formosa* on other (vegetable) host plants of *T. vaporariorum*, the experiments at 20 °C were also carried out on sweet pepper (*Capsicum annuum*, cultivar 'Westlandse-Zoete') and tomato (*Lycopersicon esculentum*, cultivar 'Moneymaker'). To determine the walking speed of *E. formosa*, video recordings were made while the females were walking on leaves of an age where hosts in the suitable stage for parasitization would normally occur. Every record was made with one individual parasitoid and with a fresh leaf placed upside down into a petri dish of 51 mm diameter. On the leaf a perspex ring of 24 mm inner diameter was placed to create a fixed searching arena. A female was transferred carefully into the arena, the petri dish was closed and mounted with the leaf upside down on a burette holder. The leaf had an upward tilt of approximately 50 percent to mimic the natural position of leaves on the plant. Recordings were started after a four minute period. The video recordings were played back on a monitor and the walking tracks of *E. formosa* were drawn on transparent sheets of plastic, with a cross mark at each 10 second interval. The tracks were then read as continuous 10-second pieces into the computer with an x-y digitizer (with a tablet of 10 coordinates per mm). Computer analysis of the tracks resulted in the average distance covered per unit of time. Periods when wasps were walking on the perspex ring or standing still were omitted from the analysis. Experiments were done in a controlled climate room at 20 °C ±1 (all cultivars, sweet pepper and tomato), 25 °C ±1 (cultivars 'Macho', 'Party' and 'Tennessee') and 30 °C ±1 (cultivar 'Parade'), respectively and a relative humidity of 70 % ± 10. Differences in walking speed on the cultivars were tested with Kruskall-Wallis (a = 0.05) followed by a multiple comparison test.

Walking pattern

To describe the walking pattern of *E. formosa* the walking track of the female wasps were compared with a lattice work of 1x1 mm and it was checked how often the path crossed a certain quadrant of the lattice. A crossing could occur nil times, once, twice, three or more times for a certain wasp. The total number of quadrants visited per recording was set 100 %, to be able to calculate a relative value of the sinuousity of that track. The tracks of all females tested on one *Gerbera* cultivar were pooled.

RESULTS

1. Leaf hair density, hair length and trichome shape

The number of trichomes per cm^2 per cultivar and their length is given in Table 1. A large variation in hair density is seen among the ten tested cultivars:

from 80 up to 1041 trichomes per cm^2. With regard to the hair density three significantly different groups of cultivars could be distinguished. All trichome lengths exceeded 0.6 mm, which is the height of *E. formosa*. The hair length varied from one to two mm outstretched. No subdivision in hair length groups was made; distinct groups were not found.

The hair shape varied considerably: (i) single and erect (Figure 1) or (ii) coiled (Figure 2) or they were entangled with each other (Figure 3). Cultivars were classified according to four trichome categories (Table 2). Glandular hairs were not found among the tested cultivars.

Table 1. Density and length (mm) of hairs on fully grown leaves of different *Gerbera* cultivars. Different letters in a colum indicate significant differences in hair density or in hair length between the cultivars by the Kruskal-Wallis test, $p < 0.05$, followed by a distribution-free multiple comparison test.

Cultivar	No. trichomes/cm^2 (x ± *sd*)	*n*	Hair length (mm) (x ± *sd*)	*n*
Macho	80.0 ± 42.0 a	20	1.2 ± 0.4 abd	100
Irmgard	100.1 ± 37.2 a	20	1.9 ± 0.1 bcd	100
Fame	111.7 ± 39.4 a	20	1.6 ± 0.4 bd	100
Provence	122.7 ± 32.9 a	20	1.5 ± 0.2 b	100
Pacific	131.1 ± 25.4 a	20	1.6 ± 0.1 abcd	100
Dragon	251.4 ± 59.6 b	20	1.3 ± 0.3 abd	100
Estelle	251.4 ± 60.9 b	20	2.0 ± 0.3 c	100
Parade	338.3 ± 93.3 b	50	1.8 ± 0.2 cd	100
Tennessee	363.0 ± 81.1 b	20	1.0 ± 0.3 a	100
Party	1041.3 ± 210 c	20	1.8 ± 0.4 bcd	100

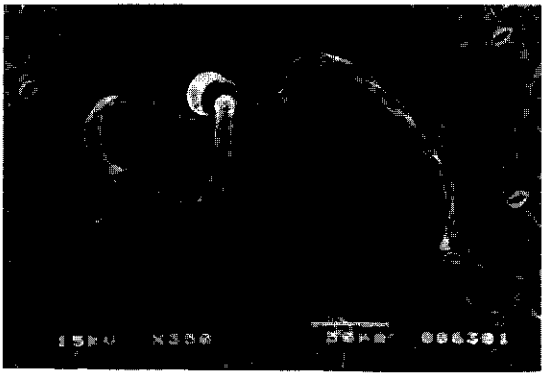

Figure 1:
Leaf surface with a trichome of the *Gerbera* cultivar 'Tennessee' (magnitude: 350 times). The cultivar belongs to the category A (simple).

Figure 2:
Leaf surface with a trichome of the cultivar 'Irmgard' (magnitude: 350 times). 'Irmgard' has twisted hairs that are bent close to the surface as described for category B (low web).

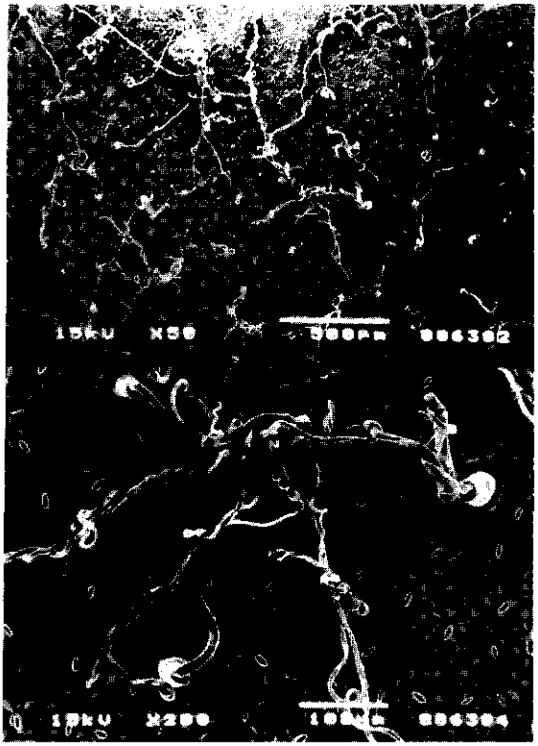

Figure 3:
Leaf surfaces with trichomes of the cultivar 'Party' (magnitude: 200 and 50 times, respectively). Trichomes are coiled and entangled in each other, the cultivar is of the D-category (complex).

Table 2. Categories of hair shape in eight *Gerbera* cultivars.

Category	Description	Cultivar
A (simple)	single trichomes, apart from each other	Fame Macho Tennessee
B (low web)	both, single trichomes and trichomes that are coiled, close on the leaf surface	Estelle Irmgard
C (high web)	both, single trichomes and trichomes entangled in each other above the leaf surface	Dragon Parade
D (complex)	a large density of the high web-type trichomes	Party

2. Searching behaviour of E. formosa

(i) Walking activity

The walking activity was calculated per wasp per cultivar from the behaviour observations. A large coefficient of variation between 0.3 and 0.4 was found per parasitoid per cultivar. The mean walking activity of all tested wasps per cultivar is given in Figure 4. In six cultivars the walking activity was between 70 and 80 percent. On cultivars 'Irmgard' and 'Party' this activity was considerably lower, i.e. 60 percent. To investigate a global slowing-down effect in the locomotion of parasitoids as a result of a certain hair density and shape, the relationship between a low walking activity and a low walking speed of individual wasps on a certain cultivar was checked. 135 wasps were tested on all cultivars. 32 females had a walking activity lower than 50 percent. Of the 32 'low activity' females, 14 had a walking speed lower than the mean speed on that cultivar and 18 a higher walking speed. So, *E. formosa* with a low walking activity were not necessarily slow walkers.

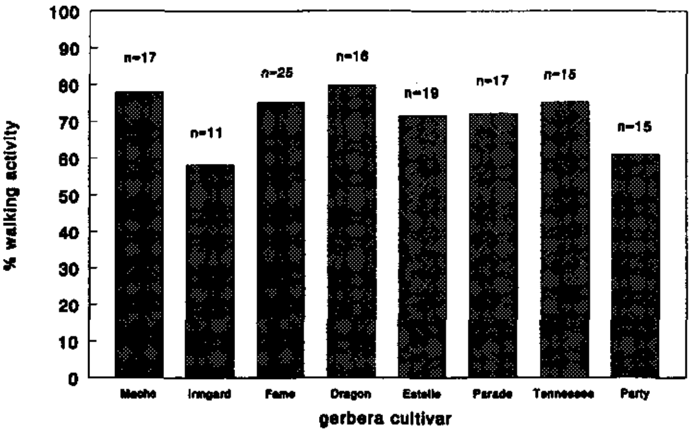

Figure 4. Walking activity (%) of all *E. formosa* females per *Gerbera* cultivar on eight *Gerbera* cultivars at 20 °C. Number of wasps (n) used is given per bar.

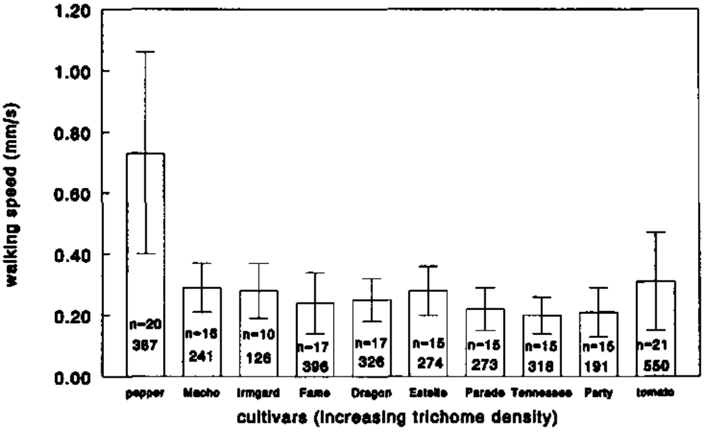

Figure 5. Mean walking speed of *E. formosa* on eight *Gerbera* cultivars, sweet pepper and tomato. The leaf hair density of the plants increases from the left to the right (vertical bars: standard deviations). The number of females and the number of 10-second pieces used are given per bar.

(ii) Walking speed

The range of walking speed of *E. formosa* on different *Gerbera* cultivars was small and varied between 0.2 mm/s and 0.3 mm/s at 20 °C (Figure 5). A significant difference in walking speed was found only between cultivar 'Tennessee' and cultivars 'Macho' (Kruskal Wallis, p = 0.01 and Mann Whitney U-test, a = $1.79*10^{-3}$ and p = 0.003) and 'Estelle' (Kruskal Wallis, p = 0.01 and Mann Whitney U-test, a = $1.79*10^{-3}$ and p = 0.004), respectively (Figure 5). The mean walking speed on *G. jamesonii* cultivars at 20 °C was 0.25 mm/s ± *sd* 0.035. Wasps tested on the *Gerbera* cultivar 'Macho', with the lowest leaf hair density, did not have a significantly higher walking speed compared to six other cultivars. A negative relationship between hair density and walking speed could not be established for *Gerbera* (Figure 5 and Table 1). On the hairless sweet pepper plants the wasps had a significantly higher walking speed; 0.73 mm/s ± *sd* 0.33 (Mann Whitney U-test, $p << 0.001$). On tomato the walking speed (0.31 mm/s ± *sd* 0.16) was the same as on the *Gerbera* cultivars. However, the hair density of tomato is above 1900 trichomes per cm^2 (Hulspas-Jordaan & van Lenteren, 1978) and much higher than found on the *Gerbera* cultivars.

With increasing temperature a significant increase in walking speed of the wasps was measured from 20 °C to 25 °C and to 30 °C, respectively (Mann Whitney U-test, $p_{20\text{-}25} > 0.04$; $p_{20\text{-}30} >> 0.01$). At 20 °C and 25 °C the walking speed was not significantly different between the tested *Gerbera* cultivars (Table 3).

Table 3. Mean walking speed (mm/s) of *Encarsia formosa* at three different temperatures on four *Gerbera jamesonii* cultivars. Number of parasitoids used and total number of 10 s tracks are given in brackets. Different letters, either within a row or within a colum, indicate significant differences (Kruskal-Wallis and Mann-Whitney-U test).

Temperature (°C)	20	25	30
Cultivar	**Walking speed (mm/s) ± sd_{n-1}**		
Macho	0.29 ± 0.080 a	0.40 ± 0.130 c	
	(16; 241)	(20; 491)	
Parade	0.22 ± 0.073 ab		0.38 ± 0.141 c
	(15; 273)		(12; 177)
Party	0.21 ± 0.081 ab	0.43 ± 0.157 c	
	(15; 191)	(20; 396)	
Tennessee	0.20 ± 0.059 b	0.35 ± 0.126 c	
	(15; 318)	(20; 420)	

Table 4. The relative occurrence of a wasp crossing its own walking path and the mean number not crossing its path on eight *Gerbera* cultivars. The mean absolute numbers of matrix cell crossings and the standard deviations SD_{n-1} are given. The number of walking paths used are given in brackets.

Cultivar	Relative occurence of crossing its own path			Mean total number of matrix cells crossed	
	0	1	≥2	(x ± *SD*)	(*n*)
Macho	0.9692	0.0303	0.0004	251.69 ± 37.38	(19)
Irmgard	0.9850	0.0151	0.0000	206.70 ± 27.91	(10)
Fame	0.9571	0.0412	0.0017	297.78 ± 35.17	(18)
Dragon	0.9725	0.0273	0.0002	247.88 ± 30.98	(17)
Estelle	0.9771	0.0219	0.0010	276.61 ± 51.64	(15)
Parade	0.9663	0.0332	0.0001	253.13 ± 47.41	(15)
Tennessee	0.9820	0.0177	0.0003	230.21 ± 24.00	(15)
Party	0.9781	0.0214	0.0004	134.95 ± 23.06	(18)
Sweet pepper (Westl. Zoete)	0.9776	0.0221	0.0002	28.30 ± 68.69	(20)

(iii) Walking pattern

The sinuosity of the walking pattern on *Gerbera* is very low. The straightness of the walking paths on all *Gerbera* cultivars was the same (arcsinus transformation). The path of a female is rather straight, as the fraction not crossing their own walking path illustrates (Table 4). Crossing their own path once or twice occurs in a maximum of 3 percent per cultivar and is, thus, negligible.

DISCUSSION

The patterns of the entangled trichomes are structures a parasitoid meets during the search for hosts on a leaf. The fully stretched length of one *Gerbera* hair is not important for *E. formosa*, simply because straight hairs were hardly found. Also a glandular-type trichome was not detected among the tested cultivars. No documentation was found on the existence of glandular hairs on leaf surfaces of *Gerbera* cultivars. Therefore, emphasis was put on the shape of hairs and the patterns they form. In spite of the large difference in trichome shape and density, the walking activity of *E. formosa* females on the *G. jamesonii* cultivars was uniform on six cultivars (72 to 80%). The lower walking activity, approximately 60%, of the parasitoid on cultivars 'Irmgard' and 'Party' cannot be explained, as expected, by a general large hair density of these cultivars or by belonging to the the same category of trichome shapes. In general, the walking activity of the wasps was relatively high in the experiments described here. However, only the first ten minutes of the searching period of a wasp were considerd. In other experiments, where parasitoids were able to stay as long as they choose on a leaf (several hours), the walking activity was 62% on cultivars 'Fame' and 'Parade' without hosts (Sütterlin et al., 1993). On whitefly infested *Gerbera* leaves a walking activity of 60% was measured during a 1.5 hour period on a leaf of the mentioned cultivars (Sütterlin & van Lenteren, 1993). On tomato the wasp's walking activity of 70% was reported to be relatively constant, during searching and after encounters with hosts and ovipositions. Also temperature did not affect the walking activity (van Roermund & van Lenteren, 1995). On *Gerbera*, a low walking activity of a female did not imply a low walking speed of that individual. In general, 'slow locomotion'- parasitoids could not be detected. This is not reported for other host plants.

The large difference in trichome density (a factor of 13) and shape did not reveal a wide range in the walking speed of the *E. formosa* females on the *G. jamesonii* cultivars. For two cucumber cultivars of different hair densities, one cultivar having half the trichomes per cm^2 as the other, Li et al. (1987) report 0.1 mm/s difference in the walking speed of *E. formosa*. That no negative linear relationship between walking speed and hair density was found on *Gerbera*, is in contrast with cucumber, where hairless, half-haired and 'hairy' cultivars were tested (van Lenteren et al., 1995). Also, no relationship was found between *G. jamesonii* trichome shape and walking speed. In the shape category A (simple) and category B (low web), for example, both was found: cultivars with higher and lower walking speed and high and low hair densities. On the hairless, smooth sweet pepper plant, cultivar 'Westlandse Zoete' a significantly different, much higher walking speed of the wasps was found compared to all *Gerbera* cultivars. The walking speed on sweet pepper (0.73 mm/s) resembles the walking speed of *E. formosa* as measured by van Lenteren et al. (1995) on hairless cucumber (0.65 mm/s). This may illustrate that leaf hairiness in general hampers the parasitoid. That hairiness can slow down parasitoids was also shown for *Trichogramma exiguum* on four different plant species, the walking speed was much lower on woolly mullein (2.6 cm/min) compared to maize (12.4 cm/min) (Keller, 1987). The walking speed of *E. formosa* on *Gerbera* at 20 °C, between 0.2 and 0.3 mm/s, is lower than on half-haired cucumber, 0.40 mm/s (van Lenteren et al., 1995) or sweet pepper. The walking speed on *Gerbera* is not significantly different from the speed on tomato, where biological control of the greenhouse whitefly with *E. formosa* is succesfully applied (van Lenteren & Woets, 1988). However, the walking speed of *E. formosa* on tomato (van Roermund & van Lenteren, 1995) at different temperatures tends to be a little higher than on *Gerbera* cultivars. The walking speed does increase with temperature between 20 and 25 °C on *Gerbera*, which was also found on tomato (van Roermund & van Lenteren, 1995). The increase in walking speed at this temperature range may be of importance for the success of biological control in a glasshouse environment where such temperatures occur almost daily for several hours. Walking speed is a very important parameter influencing the percentage parasitism of *E. formosa* on tomato plants. This is reported for the leaf level and the "crop" level (van Roermund et al., 1997 (a) and (b)). An increase in hair density leads to a decrease in encounter probability and encounter rate of *E. formosa* on cucumber (van Lenteren et al., 1995). On the same host plant, the time spent on a leaf by *E. formosa* until the first encounter of a host was significantly less on a cultivar with half the hairs per cm^2 compared to a 'standard' cultivar (Li et al., 1987). Parasitism, host feeding and the total number of whitefly hosts killed by four different *Encarsia* species were compared on two poinsettia cultivars differing in hairiness (Heinz & Parrella, 1994). The three parameters were greater on the poinsettia cultivar with a 15 % lower trichome density for all four *Encarsia* species. An inverse relationship between cotton trichome density and parasitism is also reported of *Heliothis* eggs parasitised by *Trichogramma* wasps (Schuster and Calderon, 1986). Bigler et al. (1988) report that travel speeds of *Trichogramma maidis* strains are positively related to the potential for parasitism in the field. How the presence of whitefly hosts on different *G. jamesonii* cultivars could influence the searching and walking behaviour of *E. formosa* will be discussed elsewhere (Sütterlin & van Lenteren, 1999).

The relatively straightness of the walking path of *E. formosa* on *Gerbera*, the third investigated characteristic of walking behaviour in this paper, is not altered by the different leaf surfaces of the cultivars. Li et al. (1987) report the same for *E. formosa* on two cucumber cultivars. The turning rate of the parasitoid *T. exiguum* was influenced by the leaf surface of different plant species (Keller, 1987). On maize, with erect trichomes arranged in rows, the walking paths had long straight sections, while on woolly mullein with forked trichomes and a dense pubescence the turning rates were greater (Keller, 1987). On some *G. jamesonii* cultivars, the

E. formosa walked possibly on top of the dense pubescent layer of entangled trichomes, and were not hampered in choosing a direction of the path. In absence of hosts or host derived factors, on a smooth paper disc, another *Encarsia* species, *E. deserti*, had a straight walking path with few turnings. After encountering host honeydew the rate of turning of *E. deserti* increased by a factor four and the parasitoid returned more often to the honeydew contaminated spot (Shimron et al., 1992).

In conclusion: the leaf hairiness of *Gerbera* cultivars is not a complicating factor for the searching behaviour of *E. formosa* on leaves. All the results point in the direction that biological control of *T. vaporariorum* with the parasitoid *E. formosa* should be possible on *Gerbera.*

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CHAPTER 5

PRE- AND POST-LANDING RESPONSE OF THE PARASITOID *ENCARSIA FORMOSA* TO WHITEFLY HOSTS ON *GERBERA JAMESONII*

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ABSTRACT

One of the factors that may complicate biological control of the greenhouse whitefly on Gerbera jamesonii by Encarsia formosa is the rosette shape of this ornamental, which differs from the vertical shape of most vegetable plants (cucumber, egg plant, tomato, etc.). Therefore, host-habitat location and the behaviour prior to landing on uninfested and infested leaves was studied. Attraction of E. formosa from a short distance by infested leaves could not be detected: the parasitoid females landed at random on uninfested and infested leaves. After the first landing, a redistribution of the wasps occurred on the leaves. After 24 h three times as many wasps were found on the infested leaves than on uninfested ones. In a dispersal experiment with four plants, E. formosa appeared to have no preference for landing on leaves of the medium age class, which is the age class on which most of the whiteflies in a suitable stage for parasitism occur. Twenty percent of the parasitoids were found on the plants 20 min after releasing them. These results were independent of the plant cultivar and the host density on the plants. In the course of 8 h, the number of E. formosa females recovered from plants increased linearly, and this increase was greater on plants where hosts were present and also greater on the plant cultivar with the lowest trichome density. After 24 h, the percentage of females was highest (56 %) on plants with the highest host density. E. formosa females were arrested on leaves where hosts were present. Contrary to our expectation, the results from the two G. jamesonii cultivars that differed strongly in leaf hairiness were not significantly different in most experiments. Only at the high host density was parasitism found to be lower on the cultivar with the higher hair density. Parasitoids may walk on top of the 'hair coverlet' of cultivars with high trichome density and, therefore, be hampered less than expected.

INTRODUCTION

Biological control of whitefly is currently used on a large scale in most greenhouse vegetable crops in The Netherlands (van Lenteren, 2000). Also in ornamentals, biological pest control is desirable in order to reduce the abundant use and strong dependence on pesticides. Research for development of biological control of whitefly has been initiated a decade ago on *Gerbera jamesonii* Hook (Asteraceae) (Sütterlin et al., 1990).

The relationships between the greenhouse whitefly *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae) and its parasitoid *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) have been studied intensively on vegetable host plants in order to develop and improve biological control programmes (e.g. van Lenteren, 1995; Noldus & van Lenteren, 1990). Based on the studies in vegetables (van Lenteren et al., 1995), we can predict that two factors may hamper biological control of *T. vaporariorum* on *Gerbera*. One is the structure of the leaf surface of *Gerbera* and in particular the density, length and shape of leaf hairs, which might influence the walking speed and pattern and thus the searching efficiency of *E. formosa* (Sütterlin & van Lenteren, 1997; Sütterlin & van Lenteren, 1999). The other is the plant architecture of *Gerbera*. The rosette shape of this plant (instead of a vertical shape as in most vegetable crops) might influence the dispersal of, and thus the parasitization by, *E. formosa*.

Research on the dispersal and distribution of whitefly on *Gerbera* showed that *T. vaporariorum* adults have a clear preference for the young leaves, both for feeding and oviposition (Sütterlin et al., 1991) and this preference is similar on vegetables (van Lenteren & Noldus, 1990). As a result of this oviposition preference, the host stages preferred by *E. formosa* for parasitization (L3, L4, and prepupa) are located on the older, full grown leaves. An important question is whether *E. formosa* is capable of detecting these hosts in a *Gerbera* crop before landing on the plant. Long-range searching capabilities for suitable hosts by means of volatile infochemicals is well documented in other parasitoids (see Vet & Dicke, 1992). Many parasitoids and predators are known to discriminate between uninfested and herbivore-infested plants before landing. Long-distance host location is achieved through cues from the plant and/or through indirect and direct cues from the host (Godfray, 1994). Reaction to long-distance cues may result in shorter search times, which in turn can lead to high attack rates. It has been argued that in order to maximize reproductive success, the attack rate of a parasitoid should be maximized (Vet & Dicke, 1992).

Little is known about the factors that influence the dispersal of *E. formosa* in a crop. Ledieu (1976), Hussey et al. (1976) and Madueke (1979) performed dispersal experiments in vertically orientated vegetable crops in greenhouses. They claimed that *E. formosa* is capable of detecting whitefly infested areas within a crop from a distance, and that once *E. formosa* females have arrived at an infested spot they do not readily move onto other plants. Females were found more often on heavily infested plants than lightly infested ones. They suggested that detection from a distance is probably due to attraction by the honeydew that is excreted by whiteflies. Noldus & van Lenteren (1990) re-examined this searching behaviour of *E. formosa*, using a wind tunnel and an olfactometer. They concluded that *E. formosa* is not capable of distinguishing infested from uninfested tomato plants from a distance and that wasps probably find infested leaves through random landings. Recently, Guerrieri (1997) and Romeis & Zebitz (1997) studied *E. formosa* flights and searching in a wind tunnel and an olfactometer, respectively. In both studies, a combination of visual and chemical stimuli was offered to the parasitoids, including plants, host-damaged plants and plant-host complexes. Guerrieri (1997) concluded that the number of oriented flights of the parasitoid towards the source increased when the host or parts of the whitefly host were present at the source. Romeis & Zebitz (1997), however, concluded after olfactometer studies that *E. formosa* is not able to detect host presence from a distance via olfactory cues, because offering the odours of a plant-host complex was not attractive, while a plant-host complex including visual stimuli was attractive to the wasps.

Once on a leaf, parasitoids were arrested after contacting honeydew or hosts (Noldus & van Lenteren, 1990; van Roermund & van Lenteren, 1995; van Roermund et al., 1994; van Vianen & van der Veire, 1988). Thus, there may be more than one explanation for a larger number of parasitoids on whitefly-infested leaves: (1) attraction of parasitoid females, (2) arrestment of females or (3) a combination of both.

The aim of the research described in this paper is to find out whether *E. formosa* is able to (1) discriminate between uninfested and infested plants before landing, (2) to discriminate between uninfested and host infested leaves from a distance and preferentially land on the latter, and (3) to search on leaves of all ages on a host plant with a rosette type of leaf architecture. The study included an analysis of the parasitoids' distribution in space and time on different *G. jamesonii* cultivars and with different whitefly densities.

MATERIAL AND METHODS

Host plants. The experiments were carried out with *G. jamesonii* plants, cultivar 'Fame' (with a low hair density of 112 trichomes per cm^2) and 'Parade' (with a high hair density of 338 trichomes per cm^2). Each plant was four to five months old and had eight leaves on average. The plant leaves were classified in three age-classes, as in previous experiments (Sütterlin et al., 1990): old, medium and young leaves. Plants were grown in a glasshouse compartment at 20-22 °C, 60 % r.h., and L16:D8 photoperiod.

Whiteflies. Trialeurodes vaporariorum was reared on cultivar 'Fame' at 24 °C, 50-60 % r.h., and L16:D8. Plants (cultivar 'Fame' or 'Parade') were infested for experiments by putting two to four previously mated whitefly female adults into small leaf cages on young leaves. After 3-24 h the cages and adult whiteflies were removed, so that the required number of whiteflies aimed for was achieved. The whitefly stages preferred by *E. formosa* for oviposition (L3 and L4) were obtained in about three weeks at 21 °C, 70 % r.h., and L16:D8. By that time the infested leaves were of medium age and full grown.

Parasitoids. Black parasitised whitefly pupae were obtained weekly on paper cards from Koppert Biological Systems, where *E. formosa* is reared on *T. vaporariorum* feeding on tobacco, *Nicotiana tabacum*. The same parasitoids are commercially available and used by growers for biological control of whiteflies. Cards were placed in glass Petri dishes and stored at 7 °C for a maximum of seven days. The emerged parasitoids were provided with a droplet of honey, and were maintained at 20 °C. Naive females (i.e., females without earlier host contact), not older than 16 h were used in the experiments. Before the experiment started, parasitoids had a light period of maximally 6 h. Just before the start of an experiment the females were aspirated into a glass vial (10 or 25 individuals) or kept individually in polysaccharide capsules for easy release.

Experimental procedure

Experiments 1 and 2; cut leaves. A white fine meshed cloth cage, 1.00 m x 0.92 m x 0.96 m , was illuminated by eight fluorescent tubes (Philips TDL 32W/84 HF) above the cage roof, which was made of insect-proof gauze. The light intensity was 1800 lux at leaf level and the temperature varied from 20.5 to 22.5 °C in the cage. Four medium-aged leaves of the *G. jamesonii* cultivar 'Parade' with similar surface and shape were cut from the plants and put in small glass water containers, just before starting the experiment. The leaves were arranged in a semi-circle (60° between leaves) 15 cm away from the parasitoid release point. Two leaves were uninfested and two leaves were infested with approximately 50 whitefly hosts (L3 and L4) each. The infestation rates were obtained as described in a previous section on whitefly rearing, without removing instars from the leaves. The position of infested and uninfested leaves was exchanged on a regular basis during and between observation days to correct for site effects. The data on leaves of either category (uninfested or infested) were therefore combined. In experiment 1, the first flight of 268 females, released in groups of three each, was observed and parasitoids started movement from the release-point one after another. In experiment 2, between 20 and 25 females were released simultaneously (11 replicates), and their position on the plants were assessed over time. This was done every 20 min during the first three hours and every 30 min during the next 5 h. After 24 h a final count was made. The distribution of *E. formosa* on the leaves in the course of 24 h is given as numbers per cm^2.

Experiment 3; intact plants. Four plants of the same cultivar were placed around a central release point in a white fine-meshed cloth cage measuring 145 cm x 71 cm x 90 cm. Parasitoids were released at the leaf-base level of the plants, but 26 cm away from the plants. Lights were placed directly above the cage which resulted in 4000 lux at the plant level and a temperature of 21 °C. The photophase was L16:D8. Separate experiments were done with two *Gerbera* cultivars ('Fame' and 'Parade'), with two whitefly infestation levels and clean plants. The control group was without whitefly infestation. The low density infestation consisted of two infested plants, each with one leaf with four whitefly hosts, so a total of eight hosts per experiment and two uninfested plants. In the high density infestation four infested plants, each with two leaves with 20 whitefly hosts were used, resulting in a total of 160 hosts per experiment. Ten wasps were released simultaneously per experiment. On cultivar 'Fame' 10 experiments were performed for the control-group and the low density group and five experiments for the high density group. On cultivar 'Parade' 13 experiments were performed for the control-group, 11 experiments for the low density and five experiments for the high density group. The dispersal of parasitoids was observed immediately after release. During the first eight hours their position in the cage was noted every 20 min for each individual, to obtain the distribution of the wasps over time. Three groups of locations were distinguished: the release point, the walls of the cage, and on the plants. Plant, leaf number and the leaf side on which the wasp was seen were also recorded. After 24 h the final positions were noted and the wasps were removed. The percentage of parasitoids observed over time was calculated per treatment and per location. The parasitization rate was determined by dissecting the host larvae looking for parasitoid eggs at the low host infestation rate, or by checking blackening pupae after nine days at the high infestation rate.

To determine whether *E. formosa* females prefer a certain leaf age, the number of times a female was observed on a certain leaf age-class of uninfested plants was noted. This number was corrected for the total leaf surface per age-class. The presence of females on the adaxial and abaxial leaf side was also noted. Preferences for leaf age and leaf surface were determined by analysis with the Chi-square test (Siegel & Castellan, 1988).

RESULTS

In experiment 1, the activities of 268 *E. formosa* immediately after release in a choice situation consisted of 59.8 % wasps flying, 29.8 % walking/hopping and 10.4 % immobile parasitoids. Of the females that flew towards the leaves, 55.7 % landed on the uninfested and 44.3 % on the infested leaves (Table 1). The frequency of females observed on unifested and host-infested leaves did not differ from the expectation that landing of females was at random on both leaf types (chi-square, $P > 0.2$). Thus, *E. formosa* does not discriminate between uninfested and infested leaves from a distance of approximately 15 cm.

The presence of females on uninfested and infested leaves was observed over a 24 h period in experiment 2. During this period the number of females per standard unit of leaf increased continuously on the host-infested leaves, whereas after an initial increase the total number of wasps remained the same on the uninfested leaves (Figure 1).

Table 1. First activity of *Encarsia formosa* after release in a cage with *Gerbera jamesonii* leaves, cultivar 'Parade' (Experiment 1)

Behaviour of females	n*	% of all tested females	% of females on leaves
Flying to:			
Uninfested leaves	49a	18.3	55.7
Infested leaves	39a	14.5	44.3
Leaf container	12	4.6	
Cage	60	22.4	
Total % females		59.8	
Walking/ hopping to:			
Release point	42	15.6	
Cage	38	14.2	
Total % females		29.8	
Immobile	28	10.4	
Total # females	268		

* Frequencies tested with chi-square test, no significant difference was found, P > 0.2

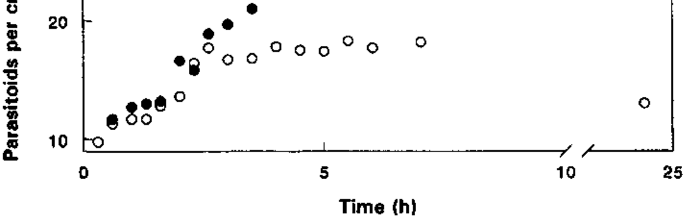

Figure 1. Number of *Encarsia formosa* per cm^2 leaf area on host infested and uninfested leaves of cultivar 'Parade' in the course of 24 h (Experiment 2).

In experiment 3, the percentage of *E. formosa* females observed on the plants calculated over all treatments, locations and observations was 73.0 % (SD_{n-1} = 5.8 %, n = 144). The percentage of *E. formosa* at the release point decreased, while the percentages in the cage increased, with the exception of a not significant, slight decrease (regression slope value = -0.16) at the high density of cultivar 'Fame' (Table 2). On the plants, the percentage parasitoids increased over 8 h on both cultivars (Figure 2 (a) and (b)). Plants having a higher host density also showed a greater increase in number and percentage of *E. formosa* females during the first eight h (Table 3). After 24 h the mean percentage of parasitoids found back on the plants was significantly different between the different whitefly densities. Analysis of variance showed a significant higher percentage of parasitoids on plants with the highest whitefly density (no hosts: 21.5 % *E. formosa* on plants, low host density: 31.8 % *E. formosa* on plants, high host density: 56.2 % *E. formosa* on plants; LSD-test, P = 0.0039).

Table 2. Relationship between percentages *Encarsia formosa* found in the cage or at the release point, and time (time intervals of 20 min.) (Experiment 3)

Cultivar	Host density	Cage	Release point
'Fame'	Control	y = 21.6 + 7.0x r^2 = 91.4 % ***	y = 58.5 - 6.1x r^2 = 93.6 % ***
	Low	y = 17.1 + 5.3x r^2 = 81.2 % ***	y = 66.6 - 8.5x r^2 = 94.6 % ***
	High	y = 33.2 - 0.16x not significant	y = 43.8 - 4.5x r^2 = 74.4 % ***
'Parade'	Control	y = 14.6 + 5.9x r^2 = 93.9 % ***	y = 75.8 - 8.1x r^2 = 96.7 % ***
	Low	y = 23.0 + 4.8x r^2 = 46.1 % **	y = 58.3 - 7.4x r^2 = 69.3 ***
	High	y = 36.8 + 2.2x r^2 = 21.1 % *	y = 51.6 - 6.8x r^2 = 87.5 % ***

Linear regression was significant with $P < 0.03$ (*), $P < 0.0003$ (**) or $P < 0.00001$ (***).

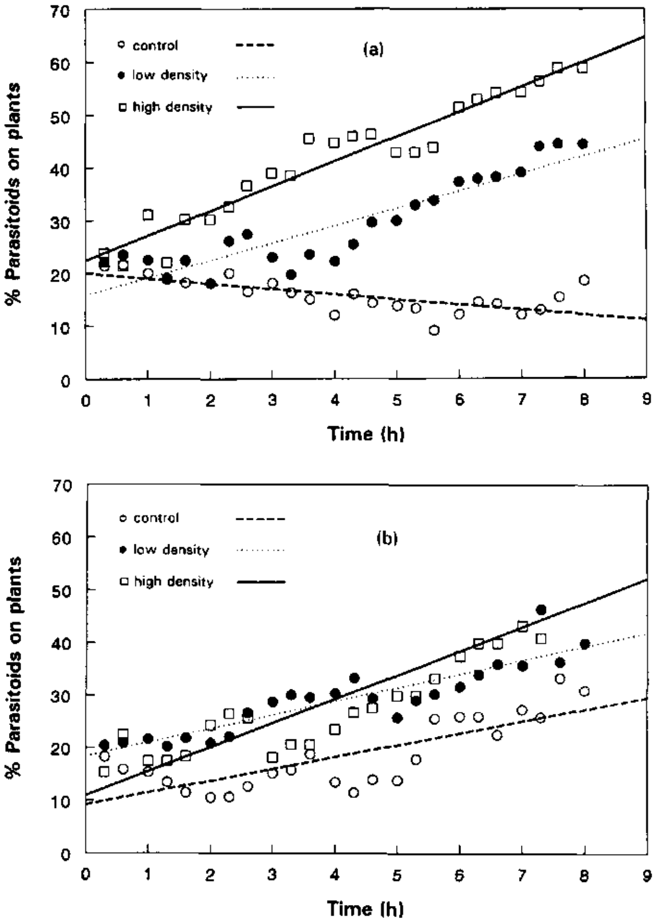

Figure 2 (a) and (b). Percentage *Encarsia formosa* on *Gerbera jamesonii* plants, cultivars 'Fame' (2a) and 'Parade' (2b), in the course of time and at three different host densities (Experiment 3). All linear regressions were significant, $P < 0.001$; when whiteflies were present the regression coefficients differed significantly from zero (t-test, $P < 0.0001$).

2 a ('Fame') Control: $y = 19.9 - 1.0x$; $r^2 = 50.1$ %
Low density: $y = 16.3 + 3.3x$; $r^2 = 81.5$ %
High density: $y = 23.0 + 4.7x$; $r^2 = 92.9$ %
2 b ('Parade') Control: $y = 9.6 + 2.2x$; $r^2 = 60.7$ %
Low density: $y = 18.7 + 2.6x$; $r^2 = 81.4$ %
High density: $y = 11.6 + 4.6x$; $r^2 = 68.2$ %

The regression slope values showed no significant differences between the two *Gerbera* cultivars and there were also no combined cultivar-density effects.

However, when testing the slopes of the linear regression at the high host density, it must be concluded that on cv. 'Fame' a significantly higher percentage parasitoids was found during the whole experimental period when compared to cv. 'Parade' (Kolmogorov-Smirnov two-sample test, $\alpha = 0.05$, $P < 0.001$). At the low host density regression slope values were different for cv. 'Fame' and 'Parade' (Table 3). However, when analyzing the percentage recaptured parasitoids in time (Figure 2(a) and (b)) with the Kolmogorov-Smirnov two-sample test we found no significant difference among the values for both cultivars ($\alpha = 0.05$, $P = 0.67$).

Table 3. The regression slope values (%/20 min) for uninfested, low and high host density plants. The linear regression describes the course of the percentage *E. formosa* re-found on the cultivars 'Fame' and 'Parade' during eight h.

	Regression slope values	
Host density	Cv. 'Fame'	Cv. 'Parade'
Control (uninfested)	-0.98^{*}a	2.24^{**}a
Low	3.25^{**}b	2.61^{**}a
High	4.67^{**}b	4.55^{**}b

Linear regressions were significant with * = $P < 0.0002$ or ** = $P < 0.00001$. Values are significantly different among different whitefly densities, when followed by a different letter (t-test with $\alpha = 0.05$).

Table 4. Number of times *Encarsia formosa* was observed on leaves sides and leaf age-classes of *Gerbera jamesonii*, cultivars 'Fame' and 'Parade' (Experiment 3)

	Control		Low density		High density	
Cultivar	Fame	Parade	Fame	Parade	Fame	Parade
No.^{1} observed	312	367	430	450	368	220
% on adaxial leaf side	25a	27a	12a	15a	11a	8a
% on abaxial leaf side	75b	73b	88b	85b	89b	92b

[1] Number of times parasitoids were observed on a leaf

Different letters within a column, indicate significant differences between chosen leaf sides (Chi-square test, $\alpha = 0.01$, $P << 0.001$). Same letters within the row, per host density, indicate no significant differences for cv.s 'Fame' and 'Parade' (Chi-square test, $\alpha = 0.01$).

% Females on leaf age-class						
Young leaves	38a	29a	29a	26a	39a	17c
Medium leaves	34a	45a	39a	48b*	29a	77d**
Old leaves	28a	26a	32a	26a	32a	6c

Different letters within a column, indicate significant differences between chosen leaf age classes (Chi-square test, $\alpha = 0.01$, $^{*}0.01 > P > 0.001$, $^{**}P << 0.001$). Different letters within a row, for the high host density, indicate a significant difference between the cultivars 'Fame' and 'Parade' (Chi-square test, $\alpha = 0.01$, $P < 0.00001$).

E. formosa searched on uninfested leaves of all age-classes without a preference for a certain age-class and about 75 % of the visits on uninfested leaves were on the abaxial (lower) leaf side (Table 4). On whitefly infested leaves (both at low and high infestation levels) the percentage of *E. formosa* present on the abaxial side was almost 90 % (Table 4). These results were not significantly different for the two *Gerbera* cultivars. On cv. 'Parade', significantly more parasitoids were observed on the medium leaf age-class compared to the young and old leaves, at both the low or the high host density.

Table 5. Number of available and parasitized hosts per treatment and number of *Encarsia formosa* females present, corrected for wasps not found

	Low density		High density	
Cultivar	'Fame'	'Parade'	'Fame'	'Parade'
No. Of available hosts	82	89	639	750
Tot. no. of parasitoids introduced	73	80	37	37
No. Of parasitized hosts	12	13	133b	65a
No. of parasitizations per parasitoid	0.2	0.2	3.6	1.8

Different letters within a row (high host density) indicate a significant difference between the cultivars 'Fame' and 'Parade' (Chi-square test, $\alpha = 0.01$, $P < 0.00001$).

The number of whiteflies on the plants and the number od parasitized whiteflies are given in Table 5. The number of parasitizations per *E. formosa* female is the same for both cultivars at the low host density. At the high host densities, significantly more hosts were parasitized on both cultivars. Further, at the high host density, significantly less parasitizations were realized per parasitoid on the hairy cv. 'Parade'.

DISCUSSION

Gerbera jamesonii leaves of all age classes were found and searched to the same extent by the parasitoid *E. formosa*, so architecture of this ornamental plant apparently forms no obstruction for *E. formosa* to locate its hosts. The preference of whitefly adults to oviposit on the newly unfolded leaves (Noldus et al., 1985; Walker & Zareh, 1990; Sütterlin et al., 1991), results in high larval (L3, L4) densities on medium aged, fully expanded leaves. A preference of the parasitoid for these leaves would reduce the time needed to find a suitable host, because of the accumulation of suitable hosts on these leaves, but such a preference was not found on uninfested plants.

Guerrieri (1997) found in wind tunnel experiments that flight was the first activity of 68.4 % of 75 tested *E. formosa* which were offered a host-plant complex. This is similar to the 60 % first flights towards plant leaves in our experiments. In the wind tunnel experiments only 24.3 % of the females landed after an uninterrupted first flight on the plant-host complex (Guerrieri, 1997), which is similar to the 33 % of the females that landed directly on the *Gerbera* leaves after the first flight in our experiment. However, when Guerrieri (1997) offered either plants or hosts, a much lower percentage (a maximum of 8 %) females landed on it.

In our experiments, the number of landings on infested and uninfested *G. jamesonii* leaves was not significantly different, so the *E. formosa* females apparently cannot distinguish between whitefly-infested and uninfested leaves from a distance in this setup. This confirms earlier data obtained in wind tunnel and olfactometer experiments with tomato plants by Noldus & van Lenteren (1990), as well as the recent olfactometer studies of Romeis & Zebitz (1997). The latter authors showed that a plant-host complex including visual stimuli was attractive, while only offering the odours of the plant-host complex was not. Those results contradict the conclusion of Guerrieri (1997) that *E. formosa* is able to locate hosts from a distance. Guerrieri (1997) worked with parasitoid females in a no-choice situation, whereas our experiments included no-choice and choice experiments. Our previous and current experiments have never indicated a preference for infested plants before landing (Noldus & van Lenteren, 1990; this paper).

A redistribution of *E. formosa* takes place over time, with increasing numbers on infested leaves, which explains the apparent misinterpretations of Hussey et al. (1976), Ledieu (1976) and Madueke (1979), that *E. formosa* is able to select infested leaves from a distance. These authors did not observe landings of individual wasps, but based their conclusion on counts of wasps on leaves.

The percentage of *E. formosa* found after release (73 %) is high in comparison to that reported by Hussey et al. (1976), Ledieu (1976), and Madueke (1979) (13-20 %). This may be due to the fact that we worked in cages, while the other authors worked in greenhouses.

The dispersal process and redistribution of females on individual leaves (Experiment 2) was comparable to the situation on leaves of intact plants (Experiment 3). Since distribution of *E. formosa* on the cultivars 'Fame' and 'Parade' was not significantly different on uninfested plants we may conclude that the large difference in hair density between these cultivars apparently has no influence on parasitoid distribution. The distribution of adult whiteflies on these cultivars was also not influenced by hair density (Sütterlin et al., 1991). On host-infested plants of the 'hairy' cultivar 'Parade', however, we found more parasitoids on the leaf age-class medium, compared to the other leaves. Females might be arrested more on hairy, host-infested leaves.

During the first hours few parasitoids landed on the plants, but landing increased later on (Experiment 3). The percentage increase of parasitoids on infested plants was greater than on uninfested plants. Parasitoids were observed more often on the underside than on the upper side of infested and uninfested leaves. On tomato, however, females showed no preference for the adaxial or abaxial leaf side on uninfested leaves, but were arrested on the abaxial leaf side after encountering hosts (van Roermund et al., 1994; van Roermund & van Lenteren, 1995). Arrestment after encountering hosts on the leaf underside was also observed on *Gerbera* leaves (Sütterlin & van Lenteren, 1999). Ledieu (1976), Hussey et al. (1976) and Madueke (1979) mentioned that *E. formosa* does not readily move on once it had arrived at an infested site. In a simulation study on tomato, van Roermund et al. (1997), showed that staying longer on the lower leaf side where hosts are normally present, results in a higher number of host encounters and ovipositions.

In the present experiment, not all hosts on visited leaves were parasitized after 24 h. Apparently parasitoids failed to encounter and parasitize all hosts in the short exposure period of 24 h. In the intact plant situation (Experiment 3), we found at the highest host density a higher percentage parasitoids on the leaves, and more parasitizations per parasitoid on the less hairy cv. 'Fame', compared to the hairy cv. 'Parade'. This might indicate that on cultivars with high hair density the host searching behaviour of *E. formosa* is hampered.

In conclusion it can be said that: (1) the parasitoids did not discriminate between uninfested and host-infested plants, and did not discriminate between uninfested and host-infested leaves prior to landing, (2) in spite of the rosette shape and different plant architecture of *G. jamesonii* compared with vegetables, *E. formosa* parasitoids visited and searched leaves of all age classes, and (3) differences in leaf hairiness of cultivars did not influence parasitism at a low host density. However, at a high host density the number of parasitizations per parasitoid is 50 % lower on the cultivar with a high hair density.

Over all these results are promising, because if neither the special plant architecture of *G. jamesonii* (this study), nor the hairiness of the leaves of *G. jamesonii* (Sütterlin & van Lenteren, 1997) are barriers to the location and parasitization of whiteflies, biological control of whiteflies might be a realistic proposition for the *Gerbera* crop in greenhouses.

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CHAPTER 6

FORAGING BEHAVIOUR OF THE PARASITOID *ENCARSIA FORMOSA* ON *GERBERA JAMESONII* LEAVES

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FORAGING BEHAVIOUR OF THE PARASITOID *ENCARSIA FORMOSA* ON *GERBERA JAMESONII* LEAVES

ABSTRACT

Insight in the foraging behaviour of the parasitoid Encarsia formosa Gahan for whitefly hosts was gained by continuous observation of individual parasitoids on leaves of the ornamental plant Gerbera jamesonii, until females left the leaf. Comparison of the parasitoid behaviour on three cultivars gave similar results. Mean searching time on uninfested G. jamesonii leaves of three cultivars was 1h 30 min and the mean percentage of walking activity of the total observation time on those cultivars was 61 %. Both parameters were not influenced by different leaf structures of Gerbera cultivars. Encounters with hosts arrested the parasitoids on the leaves. The walking activity and the percentage of host encounters that resulted in an oviposition decreased with decreasing egg load of the parasitoid.

In comparison with tomato, where biological control of whiteflies is successful, only minor differences in the foraging behaviour occur, except for the residence time of females, which was about three to four times longer on G. jamesonii leaves, but these leaves are about seven times larger than tomato leaves.

The facts that (1) the foraging behaviour of E. formosa on G. jamesonii is independant of the cultivar, and (2) the foraging behaviour is in many aspects similar to that on tomato, suggest that biological control of whitefly on this ornamental plant is a potential option.

INTRODUCTION

Biological control of the greenhouse whitefly *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae) with the parasitoid *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) has been applied on glasshouse vegetables since the 1920s and is nowadays commercially used with success on tomatoes, cucumber and other vegetables (van Lenteren and Woets, 1988; van Lenteren, 1995). At present, biological control is desired in ornamentals as well, to reduce the abundant use and dependence on pesticides. In several countries steps have been taken to achieve this in glasshouse ornamentals (van Lenteren, 1996 and Wardlow and van Lenteren, 1993). *Gerbera jamesonii* is an attractive crop for trying out biological control in ornamentals in the Netherlands, because only the flowers are marketed and, therefore, a low density of pest insects on the leaves can be tolerated, since quality of the flowers will not be affected. Furthermore, the host-plant suitability of *G. jamesonii* for whitefly, in terms of life history parameters, resembles that of tomato (Dorsman and van de Vrie, 1987; van Lenteren and Noldus, 1990). To evaluate the success of biological control of *T. vaporariorum* with *E. formosa* in a *G. jamesonii* crop, one needs information on time allocation of the parasitoid, its encounter rates with hosts and its host acceptance. Successful parasitism, and thus suppression of the whitefly population, is closely linked to the host location capability and the efficiency of the foraging behaviour (Godfray, 1994).

Direct observations of host searching, host selection, host discrimination, parasitization and host feeding behaviour were part of an extensive research carried out for vegetables in our group in order to develop mass rearing and parasitoid release methods (van Lenteren et al., 1976 a, b; van Lenteren et al., 1980; van Lenteren et al., 1996; Nell et al., 1976; and van Roermund and van Lenteren, 1995). However, the foraging behaviour and time allocation of *E. formosa* on ornamentals has hardly been studied. Plant architecture and leaf structure can affect this behaviour and thus parasitization and host feeding rates. They determine the effectivity of the parasitoid and the success as a biological control agent. Waage (1979) studied the foraging and time allocation of the parasitoid *Venturia (= Nemeritis) canescens* in a patch of hosts (*Plodia interpunctella*). He suggested a decision mechanism for the duration of a visit in such a patch. In a behavioural model, the so-called residence time of the parasitoid is predicted and was experimentally found to increase after ovipositions. The second prediction of Waages model is, that the 'giving up time' of parasitoids on patches of different host densities will be highly variable, but the rate of ovipositions will be similar in a range of patches. This also was experimentally confirmed. Whiteflies, the hosts of *E. formosa*, are aggregated at various spatial levels in a crop, as is said for phycitid meal moths, the hosts of *V. canescens* (Xu Rumei, 1992; Waage, 1979). So, based on Waage's reasonings, an increase in residence time after host encounter and oviposition is also expected for *E. formosa* on *G. jamesonii*.

In order to reproduce, the larval parasitoid *E. formosa* has to search for greenhouse whitefly larvae on the underside of the leaves of the host plants. It hops and flies from leaf to leaf without being able to select between infested and clean leaves before landing on the leaves (Noldus and van Lenteren, 1990; Sütterlin and van Lenteren, submitted). Once on a leaf, it starts walking and drumming with its antennae in search for hosts. The leaf structure and hairiness of the host plant may hamper the searching parasitoid on the leaf in terms of its walking speed, activity and pattern (Hulspas-Jordaan and van Lenteren, 1978; van Lenteren et al., 1996; Sütterlin and van Lenteren, 1997). Also, the leaf shape and size can influence the parasitoid's searching behaviour. The species *G. jamesonii* has many cultivars with a large diversity in leaf hairiness and leaf size (Sütterlin and van Lenteren, accepted). As soon as a host is 'encountered', that is when an antennal contact with the host is made, it will be inspected with antennae and/or ovipositor. The host can be rejected after antennal contact (antennal rejection) or after ovipositor contact (ovipositorial rejection). After inserting the ovipositor into the host, it can be accepted for oviposition or for host feeding (van Lenteren et al., 1980).

Here, we quantify the foraging behaviour of *E. formosa* on different *G. jamesonii* cultivars and compaire it to the foraging behaviour of the parasitoid on tomato. In previous work, the walking behaviour of the wasps was studied on non-infested leaves of different *Gerbera* cultivars at several temperatures (Sütterlin and van Lenteren, 1997). This paper deals with the next phase of the foraging behaviour and concerns the measurement of the effect of presence of hosts on the searching and parasitization behaviour of *E. formosa*.

MATERIAL AND METHODS

Plants

G. jamesonii cultivars 'Fame', 'Parade' and 'Tennessee' were used for the experiments. The plants were three to five months old and had eight full grown leaves. The leaf surface of the plant cultivars were different in (a) trichome density and (b) trichome shape. 'Fame' has a low hair density of 112 trichomes per cm^2 and 'Parade' and 'Tennessee' have a high hair density of 338 and 363 trichomes per cm^2, respectively. 'Fame' and 'Tennessee' have single trichomes which stand apart from each other, 'Parade' has single trichomes and trichomes entangled in each other (see Sütterlin and van Lenteren (accepted) for details). Tomato plants, cultivar 'Moneymaker' were used when four to six weeks old and with five leaves. The ornamental and vegetable plants were grown in separate glasshouse compartments at 20 - 22 °C, 60 % RH and 16L:8D.

Whitefly hosts

Two *T. vaporariorum* rearings were kept, one on *Gerbera*, cultivar 'Fame' and one on tomato, cultivar 'Moneymaker', so that insects without possible adaptation problems to a new plant species could be used for the experiments. The two whitefly rearings were located in seperate greenhouse compartments, under the following approximate conditions: temperature, 24 °C, 50-60 % RH and 16L:8D. Development from egg to third and fourth instar, the preferred whitefly stages for oviposition by *E. formosa*, took approximately three weeks.

Parasitoids

Black parasitized pupae were obtained weekly, glued on paper cards (for shipping), from 'Koppert Biological Systems', where *E. formosa* is reared on tobacco plants. Cards were placed in glass petri dishes of five cm diameter and stored at 7 °C for maximaly ten days. Emerged adults were provided with a droplet of honey placed inside the petri dish. Naive females, i.e. without earlier host contact, not older than 16 hours were used in the experiments. Just before the start of an experiment, the females were isolated individually in polysaccharide capsules for easy release on the leaf. All parasitoids were observed continuously on leaves of intact plants and their behaviour was individually recorded during the experiments.

Experimental procedure

All experiments were carried out in a climate room at 25 ± 1°C, 55 - 70 % RH with artificial lights (fluorescent tubes resulting in 5775 Lux at the leaf level). *G. jamesonii* leaves with or without hosts were cut off, placed in a glass vial filled with water and attached to an insect-free plant (one leaf per plant), on the position of full grown leaves, that is the the third to sixth leaf, counted from the youngest leaves. The plant under observation was placed in a semicircle of five clean plants of the same cultivar and species. During one observation day, the same plant and attached leaf were used. At the start of each experiment an individual female parasitoid was introduced from a polysaccharide capsule, cut into a point, on the underside of the attached leaf. The parasitoid was observed by the naked eye or with an stereo microscope. Handled hosts were removed and replaced. The number of observed parasitoids is given per experimental setup.

'Host search and parasitization' experiment (experiment 1). A set-up where the distance at release between parasitoid and hosts was standardized, sixteen whitefly larvae were glued, with a tiny droplet of a honey water solution, equidistantly in a circle of three cm diameter on detached leaf undersides of the *G. jamesonii* cultivar 'Tennessee' or leaflets of the tomato cultivar 'Moneymaker'. In the case of tomato, leaflets of intact plants were used to prevent wilting. Five behavioural elements, namely (i) walking, (ii) standing still/ eating honeydew/ preening, (iii) encountering a host/ drumming host, (iv) adopting oviposition posture and (v) host feeding were recorded on a microcomputer with the software programme 'The Observer' (Noldus, 1991). All five elements excluded each other and where time series from total observation time. Also the frequency of a certain element, as e.g. encountering a host, could be calculated from the recordings of the software programme. Single parasitoid females were released in the centre of the host circle on the leaf underside. An observation was terminated after the first host was encountered and handled, or after the parasitoid walked out of the host circle. Parasitoids were removed then. This means that the total observation time was not fixed and depended on the parasitoids behaviour. After the observation, the encountered hosts were dissected, checked for the presence of parasitoid eggs.

In this way 146 females were tested on leaves of *G. jamesonii* and 125 females on leaflets of tomato. Parasitoids that did not move for one hour or flew away before an encounter occurred were not considered for further analysis.

'Host encounter until first acceptance' experiment (experiment 2). High host densities of more than 100 individuals per leaf were obtained on *G. jamesonii* (cv. 'Tennessee') and tomato plants by allowing mated female whiteflies to lay eggs freely on leaves of an intact plant during 24 hours. The procedure for attaching a leaf to the observation plant and for recording the parasitoid's behaviour on the leaf was the same as as mentioned in the previous section. *E. formosa* females were released individually near a host cluster (each female near a new cluster of unparasitized hosts) and as soon as the first host was encountered and handled, the parasitoid and the host were removed and the experiment finished. In experiment 2, 87 females were tested on leaves of *G. jamesonii*, cv. 'Tennessee', and 79 parasitoids on tomato leaflets; all females encountered a host. The host was dissected and checked for a parasitoid egg.

'Time allocation on leaves with hosts' experiment (experiment 3). Host densities of approximately 20 hosts per leaf on cultivars 'Fame' and 'Parade' and of 30 hosts per leaf on cultivar 'Tennessee' were obtained by allowing mated females to lay eggs during 4 hours. For climate conditions see the above section on plant rearing. The experiment took place in spring (half February until June) for the cultivars 'Fame' and 'Parade', and in summer (July and August) for the cultivar 'Tennessee'. The observation and recording procedure was used as described above, but in this case the exact location of *E. formosa* on the leaf was added: underside of leaf, edge of leaf underside, upperside of leaf and edge of leaf upperside. The edge of the leaf was defined as the width of the parasitoids' searching path (0.5 mm). The parasitoids were observed either until they left the leaf, or stood still for a period longer than one hour, or for a maximum of 6 - 11 hours, till the lights of the climate room were turned off. A parasitoid that had not yet left the leaf after 11 hours was checked for its presence on the leaf the following morning. After each observation the encountered hosts were dissected and checked for parasitoid eggs.

We measured (i) residence time of the parasitoid on the leaf; (ii) giving-up-time, which is the time after the last host encounter until leaving the leaf, defined as hopping/flying away; (iii) host acceptance rate, which is the number of host encounters that resulted in a successful parasitization; (iv) walking activity, which is the percentage time spent walking of the total time spent on the leaf, without being in contact with hosts. All hosts on which parasitoids were in oviposition posture, but where no parasitoid egg was found, were considered 'rejected' during ovipositorial probing. We tested approximately 20 females on infested and on uninfested leaves of three cultivars 'Fame', 'Parade' and 'Tennessee'.

Statistical analyses

All data concerning behavioural differences of *E. formosa* between *G. jamesonii* cultivars or plant species were tested with non-parametric statistics. Differences between two plant cultivars or species were tested with the Mann-Whitney-U test (Siegel and Castellan, 1988) and differences between more than two cultivars were tested with the Kruskal-Wallis test (Siegel and Castellan, 1988). If further comparison among cultivars was necessary, this was performed with the Kolmogorov-Smirnov test and a Bonferoni correction (Siegel and Castellan, 1988).

Regression lines were tested with parametric statistics (t-test) (Sokal and Rohlf, 1981).

RESULTS

Host encounter and search behaviour (experiment 1 and 2):

On the two host plants, *Gerbera* and tomato, 34.9 % and 40.8 % of the females encountered a host in experiment 1 (Table 1). Much higher host densities were created in experiment 2, which resulted in a 100 percent host encounters.

Table 1. Number of *E. formosa* females tested in the host searching experiments (experiment 1) on *G. jamesonii*, cultivar 'Tennessee' and tomato, cv. 'Moneymaker'.

	Gerbera jamesonii n	Tomato n
females tested	146	125
Walking out of host circle	38	35
flying away	24	17
being inactive	33	22
Having host encounter	51	51

Table 2 shows the time until first host encounter, the handling time of the host, the time necessary for oviposition and the percentage of host acceptance for *E. formosa* on the two host plant species (experiment 1) and the host acceptance of *E. formosa* in experiment 2. The time until the first host encounter and the handling time of that host was not significantly different on *Gerbera* and tomato leaves, with the exception of the time for oviposition, which took less time on *Gerbera* (450 s) compared to tomato (730 s).

It appeared that the time a parasitoid needed to reject a host with the antennae (40 s) is 10% or less of the time it took the females for an ovipositorial rejection (578 s on G. jamesonii and 428 s on tomato). The time for an ovipositorial rejection was not shorter than the time necessary for an oviposition. Host feeding on first encounter occurred only three times, it took much longer than egg-laying. Host acceptance after the first host encounter was approximately 40 % on *Gerbera* as well as on tomato during experiment 1 and 2 (Table 2).

Table 2. Mean handling time (s) of the first host by *E. formosa* and the acceptance for oviposition (%) of the first host, on the host plants *G. jamesonii*, cultivar 'Tennessee' (Gerb.), and tomato, cultivar 'Moneymaker' (Tom.), at 25 °C. SD_{n-1}, and number of parasitoids tested are given in brackets.

host plant	time (s) (exp. 1)	handling time (s) on the first host (experiment 1)				% acceptance for egg-laying in first host	
	until en-counter	antennal rejection	oviposit. Rejection	host feeding	oviposition	exp. 1	exp. 2
Gerb.	254.1a	38.2a	577.7b	1694.8	453.2b	39.2a	40.2a
	(187.6; 51)	(53.4; 19)	(429.2; 11)	(; 1)	(259.5; 20)	(; 51)	(; 87)
Tom.	270.3a	43.4a	428.4b	1831.9	727.7c	37.3a	38.0a
	(248.7; 51)	(44.7; 15)	(383.0; 16)	(728.4; 2)	(324.8; 18)	(; 51)	(; 79)

Different letters in one section of a row indicate significant differences between handling times or % acceptance in a plant species (Mann-Whitney-U test, $\alpha=0.05$ and Kruskal-Wallis test, $\alpha=0.05$). Different letters in colums indicate significant differences between plant species (Mann-Whitney-U test, $\alpha=0.05$).

Table 3. Mean residence time (s) and walking activity (%) on leaves of three *Gerbera jamesonii* cultivars without hosts at 25 °C.

	G. jamesonii cultivar								
	'Fame'			'Parade'			'Tennessee'[1)]		
	mean	$SD_{(n-1)}$	(n)	mean	$SD_{(n-1)}$	(n)	mean	$SD_{(n-1)}$	(n)
Residence time (s)	4386.8a	±3181.1	(18)	5563.3a	±3931.9	(21)			
Walking activity (%)	66.7a	±23.0	(18)	58.8a	±24.2	(21)	58.5a	±29.6	(21)

[1)] measured on leaves with hosts, but before the first encounter with hosts

The same letters in a row indicate no significant differences between cultivars with Mann-Whitney-U test ($\alpha=0.05$) and Kruskal-Wallis test (a=0.05).

Time allocation (experiment 3):

On *Gerbera* cultivars 'Fame' and 'Parade' the oviposition time on the first host could be calculated from experiment 3. On 'Fame' only one first encountered host was accepted for oviposition and it took the female 283.5 seconds to lay the egg. On cultivar 'Parade' six parasitoids accepted their first host. The mean oviposition time was 333.1 s with a SD_{n-1} of 128.8 s.

The residence time of the parasitoids on leaves without hosts was similar on the *Gerbera* cultivars 'Fame' and 'Parade' and amounted to on average 4975.1 s (Table 3). Also, the walking activity of the females was nearly the same on both cultivars and showed a mean of 62.8 % (Table 3). On cultivar

'Tennessee' the walking activity of *E. formosa* was measured only on leaves with hosts, but we can extrapolate the walking activity on uninfested leaves by taking in account only periods before the first host was encountered. We found a walking activity of 58.5 % which is similar as that on 'Fame' and 'Parade' (Table 3).

Table 4. Mean residence time and walking activity, the number of encounters, ovipositions, host feedings and the oviposition ratio and host feeding ratio of *E. formosa* on leaves of three *Gerbera jamesonii* cultivars with 20 to 30 hosts per leaf at 25 °C. SD_{n-1} of replicates and the number of parasitoids used are given.

	G. jamesonii cultivar								
	'Fame'			'Parade'			'Tennessee'		
	mean	$SD_{(n-1)}$	n	mean	$SD_{(n-1)}$	n	mean	$SD_{(n-1)}$	n
Residence time (s) (females left leaf)	8685.5a	±6086.6	10	13027.8a	±5540.5	10	13499.9a	±7499.9	11
Walking activity (%)	47.74a	±23.84	19	45.53a	±17.88	19	39.25a	±20.54	24
# Encounters	7.4a	±7.2	19	12.2ab	±9.5	19	16.3b	±11.0	24
# Encounters of different hosts	3.8a	±4.4	19	6.5ab	±4.1	19	10.7b	±6.5	24
# Ovipositions	1.5a	±2.6	19	2.4b	±2.7	19	6.9c	±4.5	24
# Host feedings	0.2a	±0.4	19	0.8a	±0.9	19	0.5a	±0.6	24
Host feed. Ratio (%)	9.9a	±27.1	16	14.1a	±24.1	18	9.0a	±16.7	23
Oviposition ratio (%)	18.8a	±24.1	16	28.6b	±31.2	18	65.1c	±23.2	23

The same letters in a row indicate no significant differences between cultivars with Kruskal-Wallis test (a=0.05). When a significant difference was observed among the cultivars, further comparison was performed with the Kolmogorov-Smirnov test, with Bonferoni correction (a < 0.009).

The time allocation of females on infested leaves is given in Table 4. Again, the residence times on the three cultivars were not significantly different, although more time was spent on 'Parade' and 'Tennessee'. On average the time spent on a leaf by a parasitoid was 11737.7 s (3.3 hours). When hosts were encountered, the residence time was on average 2.4 times higher compared to the time the parasitoids spent on uninfested leaves. On the three cultivars with hosts the walking activity of the females was not significantly different (on average 44.2%), but lower than on leaves without hosts. During the stay on the leaf, the number of encounters with (new) hosts was lower on the cultivar 'Fame' compared to 'Tennessee'. But on 'Tennessee' about 30 hosts were offered to *E. formosa* compared to 20 hosts on the other two cultivars. Individual *E. formosa* females had up to 45 encounters with up to 26 different hosts and laid maximally 15 eggs during their stay. Of the encounters per wasp approximately 65 % were new host encounters (cv. 'Fame' 67.6 % ±26.9 n=16, cv. 'Parade' 58.3 % ±18.6 n=18, cv. Tennessee 69.1 % ±16.2 n=23). Previously encountered hosts were antennally rejected in

80 to 90 % of the cases, and only took a few seconds. Re-encountering a host occurred during the whole residence period of females and was not due to unavailability of unencountered hosts. The number of ovipositions and the oviposition ratio (percentage of new host encounters resulting in an oviposition) was considerably lower on 'Fame' and 'Parade' compared to 'Tennessee', although this was not the case for the number of host feedings and the host feeding ratio.

Table 5. Mean time periods after host encounters of *Encarsia formosa* on infested leaves of three *Gerbera jamesonii* cultivars.

Cultivar		'Fame'	'Parade'	'Tennessee'
a) time until 1st encounter (s)	mean	1590.0a	1874.3a	1023.8a
	SE	365.4	623.7	266.3
	median	1102.0	1270.7	558.5
	n[1]	19	18	24
b) successive time periods after 1st and before last encounter (s)	mean	819.3ab	802.5a	1100.8b
	SE	105.1	87.8	105.1
	median	357.4	317.3	230.3
	n[1]	135	207	326
b2) successive time periods after 1st oviposition (s)	mean	883.2a	997.3ab	1283.4b
	SE	164.7	140.4	125.3
	median	335.0	265.0	388.4
	n[1]	62	105	332
c) GUT after last encounter; females left (s)	mean	1826.6a	2889.4a	1723.8a
	SE	383.1	633.9	430.4
	median	2060.2	3572.6	1690.6
	n[1]	10	9	11
d) GUT after last encounter; females removed (s)	mean	4152.2a	5864.7a	5239.3a
	SE	451.7	946.4	1539.1
	median	3745.2	4682.0	3669.3
	n[1]	9	9	13

The same letters in a row indicate no significant differences with Kruskal-Wallis test (a=0.05). When a significant difference was observed among cultivars, further comparison was performed with the Kolmogorov-Smirnov test, with Bonferoni correction a < 0.009. GUT = giving-up times.

[1] n stands for the number of times a certain time period or behaviour could be measured.

The mean time until the first host encounter did not differ significantly on the three cultivars (Table 5). However, considerable variation per cultivar occurred. This was also the case for the giving-up time (the period of time after the last host encounter until the parasitoid left or had to be removed). The time intervals between successive encounters were different among the cultivars (Table 5): after the first encounter, the time periods were shorter on cultivar 'Parade' compared with 'Tennessee'. The time periods after the first oviposition of females were shorter on 'Fame' compared with 'Tennessee'.

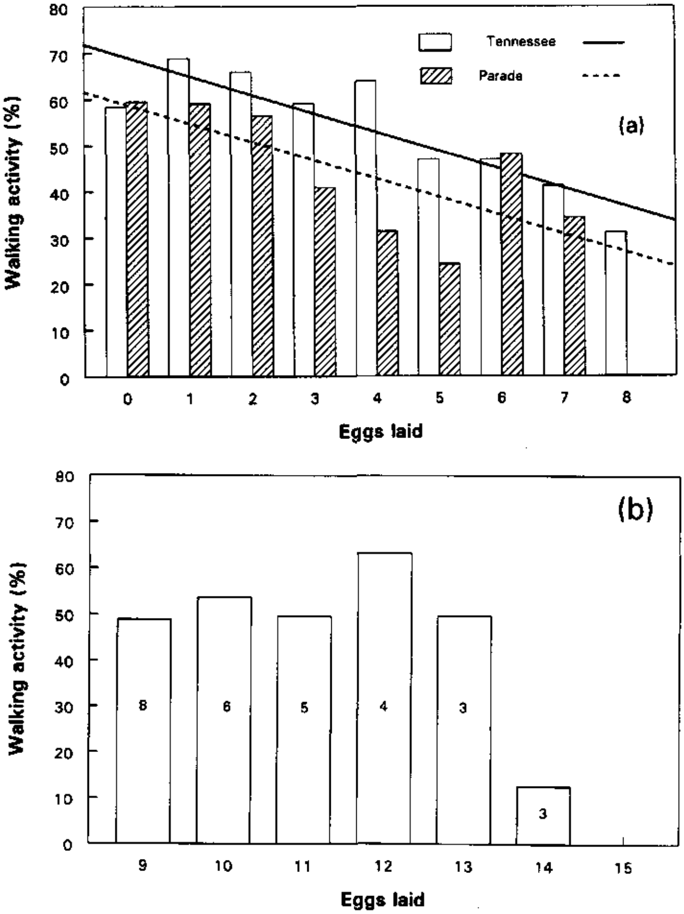

Figure 1 (a) and (b). Walking activity of *Encarsia formosa* before the first and after consecutive ovipositions on *Gerbera jamesonii* leaves. Figure 1 (a): For 0 up to 8 eggs laid by the parasitoid the number of replicates is for cultivar 'Tennessee': 21, 23, 19, 17, 18, 15, 10, 11 and 9, respectively, and for cultivar 'Parade' (0 up to 7 eggs laid): 10, 9, 8, 7, 6, 6, 3 and 2, respectively. Linear regression gave $y = 69.8 - 4.04x$ (cv. 'Tennessee') and $y = 58.3 - 4.01x$ (cv. 'Parade'), respectively. Figure 1 (b): 9 up to 14 eggs laid, cv. 'Tennessee'. Number of replicates is given per bar.

When looking closer at the walking activity and the host acceptance for oviposition in relationship to egg laying, one gets the following picture. On both cultivars, 'Parade' and 'Tennessee', the walking activity is around 60 % for the first few ovipositions, then gradually decreases to less than 40 % at the ninth oviposition. The linear decrease was significant for both cultivars; R^2 = 75.7 %, P = 0.002 (cv. 'Tennessee') and R^2 = 52.1 %, P = 0.043 (cv. 'Parade') (Figure 1a). After the eighth oviposition we observed an increase in acceptance for oviposition to about 50 %, it again decreases after the 13th oviposition (Figure 1b).

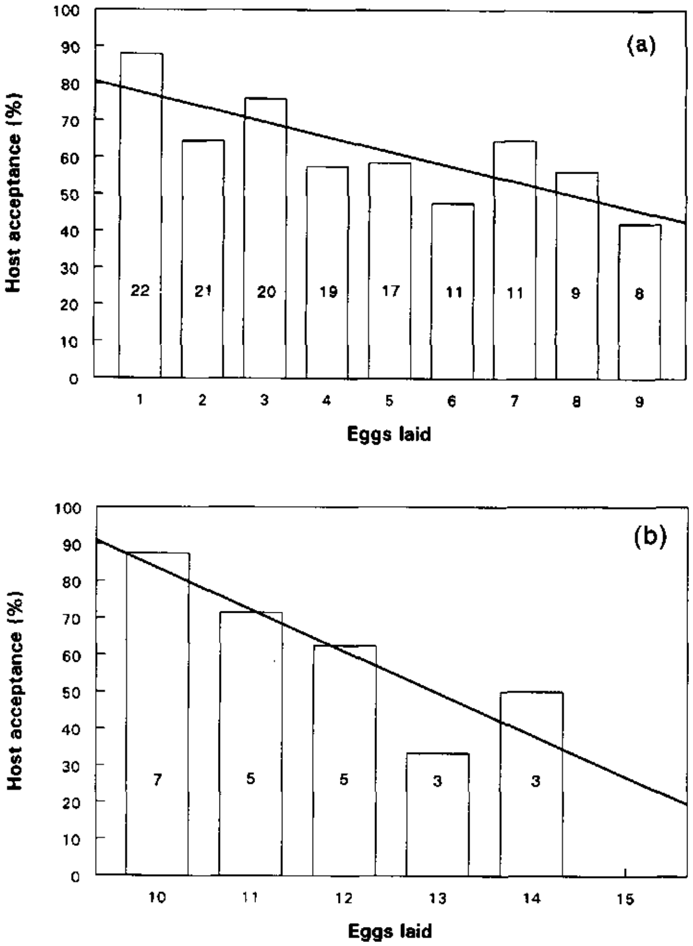

Figure 2 (a) and (b). Host acceptance for oviposition by Encarsia formosa after the first and consecutive ovipositions on Gerbera jamesonii leaves, cv. 'Tennessee'. Number od replicates is given per bar. (a) Zero to nine eggs laid; linear regression resulted in $y = 81.79 - 4.02\ x$.
(b) Ten to 14 eggs laid; linear regression resulted in $y = 96.66 - 11.31x$

DISCUSSION

The foraging behaviour for *E. formosa* on *G. jamesonii* can be summarized as follows. On leaves without hosts the females searched for approximately one and a half hours before they left. Encounters with hosts clearly arrested the parasitoid on the leaf: the mean residence time on infested leaves was about three and a half hours compared with one and a half hours on clean leaves. Residence times were similar on plant cultivars with different leaf structure and hairiness. The time parasitoids spent in searching for hosts (walking activity), was also independent of cultivars. In the presence of hosts, walking activity and host acceptance were influenced by the eggload of the parasitoid: with a high eggload walking activity and host acceptance are high and with a low eggload of the parasitoid the values for both parameters decrease.

Time allocation

Residence times of individual parasitoids have been measured on tomatos and were found to be much shorter (approximately 20 minutes) on leaflets without hosts (Van Roermund and van Lenteren, 1995). The difference in leaf size between *G. jamesonii* and tomato is probably the main cause of this difference in residence time. Fullgrown *G. jamesonii* leaves are more than seven times bigger than a tomato leaflet (300 cm^2 and 40 cm^2, respectively, measured in our experiments). However, the leaf area index of the crops (LAI) is about the same: a peak of 3 m^2 leaf / m^2 ground in the late spring with a gradual decrease to 1.5 m^2 m^{-2} measured during a period of 100 days (Heuvelink, 1996). Therefore, the fraction of leaf area of the canopy searched by the parasitoids could be about the same. Similarly to *Gerbera,* on tomato leaflets, the parasitoids were also arrested by host encounters. For patchily distributed hosts like whiteflies, this is what theory predicts (Waage, 1979), since host encounter rates and thus possibly egg laying of parasitoids increase when host density is locally high. With patches of one or a few hosts and uniformly distributed hosts, however, Driessen et al. (1995) showed for the same parasitoid (*Venturia canescens*) as studied by Waage that an oviposition decreased the time spent in a patch. On the host plants tomato and *Gerbera*, the variation in residence time was very high, which is difficult to handle quantitatively. However, van Roermund et al. (1994) analysed their foraging data (on tomato) with a proportional hazards model and leaving of the parasitoid appeared to be characterized by a constant probability per unit of time.

In the present experiment, when hosts were available, the number of females leaving the leaf within the experimental day was limited. Many females were still on the leaf at the end of the day, so giving-up times of table 5 are probably underestimated. Also, periods between successive host encounters are underestimates of the giving-up time of a parasitoid. From observations on tomato it is known that only an oviposition into an unparasitized host lengthens the giving-up time (van Roermund et al., 1994). The high variability of giving-up times found in our experiment is not uncommon for parasitoids. It is also mentioned for *E. formosa* on tomato leaflets (van Roermund et al., 1994), for *Aphidius colemani* on cucumber leaves (van Steenis et al., 1995) and for *Venturia (= Nemeritis) canescens* on wheat middlings (Waage, 1979).

Host encounter and handling behaviour

Differences in number of encounters between parasitoids and hosts on different *G. jamesonii* cultivars led to differences in number of ovipositions, with the total killing rate of hosts larger on cultivar 'Tennessee'. On each of two *G. jamesonii* cultivars, 'Fame' and 'Parade', the mean period until the first host encounter is somewhat longer than the successive periods of time between encounters with hosts. This can be explained by re-encountering of the same host after a very short time interval. For females still on the leaf at the end of the experimental day, the time since last host encounter amounted to 5000 s, which is similar to the total residence time on clean leaves (4975.1 s). Unlike the latter females, the former mentioned parasitoids are almost inactive and probably egg-depleted on a host infested leaf and were found in most cases on the same leaf even the following day.

When hosts were offered in an equidistant position from the parasitoid, the host encounter rate was the same on tomato and *G. jamesonii*, despite their difference in leaf structure. This result was expected, because only very small differences in walking activity and walking speed were found between these plant species (Sütterlin and van Lenteren, accepted). The handling time of a host depended on acceptance or rejection of the host. Both, the antennal and ovipositorial rejection times were the same for tomato and *G. jamesonii* and on the three *Gerbera* cultivars. The data for tomato were similar to those reported by Van Roermund and van Lenteren (1995). Host feeding after encountering the first host took on average four times longer than an oviposition on both host plants. The number of host feedings on the first host was limited, and this was expected (Nell et al., 1976; van Roermund et al., 1996). The time a parasitoid used for the first oviposition in a host on *Gerbera* (all cultivars) was shorter than on tomato, but other authors found shorter oviposition times on tomato (reviewed by van Roermund and van Lenteren, 1995) and similar to those on *G. jamesonii* cultivars. Our data show that a distinction between ovipositorial rejection and oviposition of *E. formosa* cannot be made on basis of the time allocation, because the handling times for those two behaviours were similar. A distinction can only be made by dissecting the whitefly larvae.

Searching behaviour and ovipositions

The average walking activity of the parasitoids on the three cultivars of *G. jamesonii* was 61 % on clean leaves and independent of the cultivar. Godthelp (1989) also found this on *G. jamesonii* (cultivar 'Fame' and 'Parade'). On cucumber leaves the walking activity was found to be around 60 percent and on tomato it was 72 percent (reviewed by van Roermund and van Lenteren, 1995). On *G. jamesonii* leaves with more than twenty hosts, the mean walking activity was around 45 percent on all cultivars. When calculated for the first ovipositions, high walking activities were found (60 to 70 percent). The walking activity decreased after circa four hosts have been encountered and eggs laid, thus, probably, with ongoing depletion of their egg load. This decreasing walking activity with eggs laid was also found for *E. formosa* when searching and ovipositing on cucumber (van Roermund and van Lenteren, 1995). A decreasing relationship of both, walking activity and host acceptance with the number of eggs laid by *E. formosa* may be based on the same relationship with the physiological parameter egg load. Such a relationship was also found for a number of parasitoids by Minkenberg et al. (1992).

In our experiments, we found an interesting aspect: the parasitoids' walking activity and host acceptance was found to increase again after eight ovipositions (Figures 1 and 2). We hypothesize this to be the result of simultaneous maturation of several eggs in the ovarioles after the first ovipositions, a process taking a certain amount of time. This hypothesis is supported by work of van Vianen and van Lenteren (1986a). They found an average of 8.9 ovarioles in *E. formosa*. Per ovariole, circa one mature egg was found half a day after emergence of the parasitoid (Kajita and van Lenteren, 1982; van Vianen and van Lenteren, 1986b). Van Vianen and van Lenteren (1986b) also observed that egg maturation rate at a certain time depends on the egg load at that time and that eggs immediately ripen after oviposition occurs. The maximum egg maturation rate at 25 °C is 0.7 eggs per hour (van Roermund et al., 1996).

In conclusion, virtually no statistical differences were found in the foraging behaviour of the parasitoid between different cultivars of *G. jamesonii* and that only small differences in the foraging behaviour occur when comparing the two host plant species. The main difference found between *G. jamesonii* and tomato was that the average residence times of parasitoids was 4.5 times longer on uninfested leaves of *Gerbera* cultivars. Because of the similarity of foraging behaviour of the parasitoid *E. formosa* on the two host plants at the leaf level combined with results found by Sütterlin and van Lenteren (submitted) for host plant location and host location, also no substantial differences are expected at the plant level. Therefore, because of the success of biological control on tomato, biological control of *T. vaporariorum* with *E. formosa* is a promising option on *G. jamesonii.*

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CHAPTER 7

BIOLOGICAL CONTROL OF THE GREENHOUSE WHITEFLY IN *GERBERA* WITH THE PARASITOID *ENCARSIA FORMOSA*: POPULATION DYNAMICS IN EXPERIMENTAL RELEASES

SUBMITTED AS:
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BIOLOGICAL CONTROL OF THE GREENHOUSE WHITEFLY, TRIALEURODES VAPORARIORUM, IN GERBERA JAMESONII WITH THE PARASITOID ENCARSIA FORMOSA: POPULATION DYNAMICS IN EXPERIMENTAL GLASSHOUSES.

BIOLOGICAL CONTROL OF THE GREENHOUSE WHITEFLY IN *GERBERA* WITH THE PARASITOID *ENCARSIA FORMOSA*: POPULATION DYNAMICS IN EXPERIMENTAL RELEASES

ABSTRACT

The effect of introductions with different numbers of *Encarsia formosa* to control greenhouse whitefly in glasshouses with a *Gerbera jamesonii* crop has been studied. Population dynamics of *Trialeurodes vaporariorum* and *E. formosa* were followed in three glasshouses of 60 m^2 with 192 plants. In the glasshouse where no parasitoids were introduced, the whitefly population increased exponentially during an 12 week observation period. The number of *T. vaporariorum* was more than 40 times lower when *E. formosa* females were released once centrally in the glasshouse with an average density of one parasitoid per plant. One central release of on average three parasitoids per plant resulted in a 120 times reduction of the whitefly population. Almost no white pupae and scarcely any adults were found at the end of the observation period in the glasshouse with the highest release rate. Also, the production of honeydew was very limited and sooty mould could not be detected. Percentage parasitism reached more than 80 % in both glasshouses with *E. formosa* releases and, once it could be detected, was never below 58 % during the experimental period.

Dispersal of centrally released *T. vaporariorum* over all 192 plants is fast. Already during the second generation whiteflies were found on every plant in the glasshouse. With a single, central release of on average three adult parasitoids per plant, good biological control of the greenhouse whitefly with *E. formosa* was achieved in this *G. jamesonii* crop. In larger, commercial greenhouses, about the same average number of *E. formosa* per plant is expected to be sufficient to control greenhouse whitefly

INTRODUCTION

Biological control of whitefly is used on a large scale in most greenhouse vegetable crops in The Netherlands and several other European countries nowadays (van Lenteren, 1995; van Lenteren & Tommasini, 1999). Also in ornamentals, biological control of pest insects is desirable in order to reduce the abundant use and strong dependence on pesticides. In many European countries such as Denmark, Germany, Italy, Sweden, The Netherlands and the United Kingdom, the introduction of natural enemies has started recently in commercial glasshouses with ornamentals (Wardlow & van Lenteren, 1993; van Lenteren, 1996, 1999).

In large glasshouses the precise effects of a natural enemy on populations of a pest insect are often difficult to measure. The climate varies among glasshouses, plant cultivars may be different, initial pest numbers differ and outbursts of pests occur at different moments. By studying pest-natural enemy-interactions in small glasshouses one may obtain good insight in the population dynamics of pest insect and parasitoid. But the results cannot simply be extrapolated to large size commercial glasshouse and, thus, careful upscaling is always needed to assess the effects of natural enemy introductions on the development of populations of pest insects in such large environments (Van Driesche & Bellows, 1996).

Dispersal of greenhouse whitefly on plants in a glasshouse, and the population dynamics of whitefly and its parasitoid *Encarsia formosa*, have been extensively studied on experimental and commercial glasshouse level in the vegetable crop tomato (e.g. Eggenkamp-Rotteveel Mansveld et al., 1982a, 1982b; Martin et al., 1991; Noldus et al., 1985, 1986; Xu Rumei, 1991). Studies of the biology and dispersal of whitefly and *E. formosa* in ornamentals have only started recently. We found that the dispersal behaviour of whiteflies on *Gerbera jamesonii* is very much comparable to the behaviour on vegetable host plants (Sütterlin et al., 1990, 1991, and chapters in this thesis; van Lenteren & Noldus, 1990). Whitefly adults prefer the young leaves for feeding and oviposition. As a result, preferred host stages for oviposition by *E. formosa* are found on fully grown leaves (Noldus et al., 1986; Sütterlin et al., 1991; van Lenteren & Martin, 1999; Xu Rumei, 1991). Laboratory research on the ornamental plant *G. jamesonii* has shown promising results concerning host finding and parasitism of whitefly by the parasitoid *E. formosa* (Sütterlin & van Lenteren, 1997, 2000). Like on other host plants, *E. formosa* is not able to locate infested leaves before she lands on the leaf (Noldus & van Lenteren, 1990; this thesis). As a result, the parasitoid searches on leaves with and without hosts and of all ages of *G. jamesonii* plants. Shortly after adult parasitoids are released, the distribution over host plants and leaves is at random, but after 24 hours a redistribution of parasitoids towards leaves with whitefly larvae does occur because females are arrested on infested leaves, while they depart from uninfested leaves (Sütterlin & van Lenteren, 2000).

All data we collected in the laboratory concerning whitefly and the parasitoid (see previous chapters) indicate that biological control in *G. jamesonii* might be possible. A logical next step is, thus, to see whether the results from laboratory can be translated to glasshouse situations. However, several problems may occur when upscaling to glasshouses, like (1) a different searching efficiency of the parasitoids as result of the larger plant size and different canopy composition compared with the laboratory situation, (2) the realization of lower parasitization efficiencies because of ever increasing plant leaf areas during the two-year growing period of the plants, and (3) an imperfect synchronization of whitefly and parasitoid development over several generations. Therefore, a number of experiments has been performed in small, experimental glasshouses of 60 m^2 before starting experiments in larger semi-commercial glasshouses of 300 m^2.

In this chapter we describe results of experiments where different numbers of parasitoids were released in glasshouses with initially similar numbers of whiteflies. Results on whitefly and parasitoid dispersal over the glasshouses, as well as percentages parasitism are presented.

MATERIAL AND METHODS

Insect rearing.

T. vaporariorum has been reared for many generations on *G. jamesonii*, cultivar 'Fame'. Rearing temperature was 24 °C ± 1 °C, the relative humidity was 50 - 60 % and light conditions were 16L:8D. The whitefly sex ratio was generally 1:1.

Parasitoids were obtained as black pupae, glued on papercards, from 'Koppert Biological Systems', where *E. formosa* is reared on greenhouse whiteflies on tobacco plants. Emerged adult parasitoids were provided with a droplet of honey. Naive females (i.e. females without earlier host contact) were used during the glasshouse experiments. Just before release of the females in the glasshouse, they were aspirated into large glass vials (maximally 100 individuals per vial), and put at stem level of four plants in the centre of the glasshouse.

Population development of T. vaporariorum *and E.* formosa.

In each of three glasshouses of 60 m^2, 192 *Gerbera* plants of cultivar 'Tennessee' were planted in three double rows on rockwool. The distance between plants in the same row was 20 cm and between plants of adjoining rows 38 cm. Relative humidity was 60 - 70 %, the temperature (set-point 20 °C) was controlled automatically via a climate computer, shading systems and screened windows. Means measured during the experimental period (summer) were 65 % RH and 21.6 °C. On very sunny days a maximum temperature of 33.4 °C was measured.

Six weeks after planting a total of 362, 375 and 390 adult *T. vaporariorum*, respectively, were released on four central plants in each of the three glasshouses (the control, the low density *E. formosa* glasshouse and the high density *E. formosa* glasshouse). This meant that on average two whitefly adults were released per plant. The day of whitefly releases was called day 0. Whiteflies were collected from the whitefly rearing shortly before release.

Three and a half weeks later parasitoids were released centrally in two glasshouses. The number of adult parasitoids released was 198 and 566, so on average one and three per plant, respectively. Weekly counts were made of whitefly adults, pupae, empty pupal cases and black parasitized pupae on a sample of the infested plants. The number of plants in the sample and their location in the glasshouse were derived from an 'incidence score method' (one or more whitefly adults per plant) of all leaves and plants. We carefully checked 50% of the plants on which whitefly adults were found for presence of whitefly and parasitoid stages. These sample data were used to estimate the whitefly and *E. formosa* populations in the glasshouses. Percentage parasitism was calculated as the number of black pupae devided by the number of black pupae plus the number of whitefly pupal cases. In the 'control glasshouse' population counts were made during a 12-week-period. In the 'low density glasshouse' popualtion counts were made during 13 weeks, and in the 'high density glasshouse' during 11 weeks.

Other pest insects like spider mites, thrips and leafminers, were successfully controlled by introduction of their natural enemies.

RESULTS

Whitefly infection determined by the incidence score

The dispersal of whiteflies within the plant rows and between the benches could be followed with the incidence score (Table 1). In the control glasshouse where no parasitoids were released we found whitefly adults on 50 % of the plants after three weeks They were concentrated in the middle double row, where they had been released. Thirty-four days after release most of plants were infested with adults, and from day 62 onwards all plants were infested.

Table 1. Percentage of *Gerbera jamesonii* plants, cultivar 'Tennessee', infested with one or more adult *Trialeurodes vaporariorum* in three glasshouses. Either no parasitoids were released (control), or a low (one *E. formosa* per plant) or high (three *E. formosa* per plant) number of parasitoids was released.

% Plants infested with adult whiteflies

Day$^{1)}$	Double row 1$^{2)}$			Double row 2$^{3)}$			Double row 3$^{4)}$		
	Control	Low E.f.	High E.f.	Control	Low E.f$^{3)}$	High E.f.	Control	Low E.	High E.f.
7	5	6	31	47	45	47	11		17
13	9	5	33	53	50	47	3		17
34	95	n.c.	n.c.	98	n.c.	n.c.	85	n.c	n.c.
46	97	77	89$^{(*)}$	100	92	85$^{(*)}$	88	6	80$^{(*)}$
62	100	n.c.	n.c.	100	n.c.	n.c.	100	n.c	n.c.
70	100	100	36$^{(**)}$	100	100	32$^{(**)}$	100	10	42$^{(**)}$
90	100	100		100	100		100	10	

$^{1)}$ = day after whitefly release

$^{(*)}$ = day 50; $^{(**)}$ = day 72; n.c. = no count

No significant differences between the first two colums of the same double rows (Kolmogorov-Smirnov, ($\alpha = 0.05$, $P^{2)} = 0.66$, $P^{3)} = 0.30$ and $P^{4)} = 0.66$)

The development in the number of plants infested with whitefly was similar to that in the glasshouse where one *E. formosa* per plant was released. Also here a concentration of infested plants occurred in the central double row during the first few weeks and then whitefly adults moved to both other double rows. The Kolmogorov-Smirnov test with which we compared the number of plants infested with whitefly adults in time in the control glasshouse and the glasshouse with a low *E. formosa* density in Double row 1, 2 and 3, respectively, showed no significant differences between the control and the low parasitoid release glasshouse (α = 0.05, P = 0.66, P = 0.30 and P = 0.66, respectively). Eventually also all plants were infested in the glasshouse where one *E. formosa* per plant was released.

In the glasshouse where three *E. formosa* were released per plant, whiteflies were found on 85% of the plants after four weeks. However, the number of infested plants decreased steadily. On half of the plants whitefly adults were observed on day 63 and on day 79 (last incidence score) only one third of the plants were infested with whitefly adults. Infested plants were then found uniformly over all double rows, contrary to the situation in the first weeks after whitefly release.

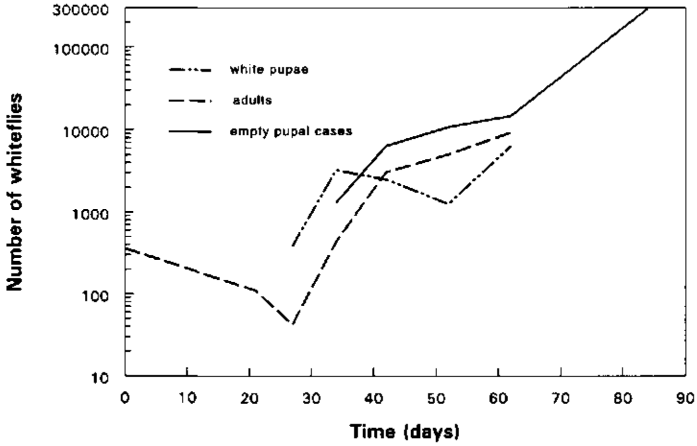

Figure 1. Population growth of *Trialeurodes vaporariorum* (white pupae, empty pupal cases and adults) on 192 *Gerbera jamesonii* plants during 84 days.

Whitefly and parasitoid population counts

The number of *T. vaporariorum* adults, pupae and empty pupal cases increased steadily in the control glasshouse (Figure 1). The increase of empty pupal cases during the experimental period of 84 days could be described by an exponential growth curve (y = 10 exp (4.1 + 0.1x)), a regression coefficient of 0.1 day^{-1}, and a coefficient of determination (r^2) of 0.95. The population reached a level of on average 1528 pupal cases per plant, and a total number of almost 300,000 for the whole glasshouse at the end of the experiment. Over the whole experiment, the mean number of whitefly adults per plant was 486.

In the glasshouse where on average one *E. formosa* was released per plant, counts of pupal cases were much lower compared to the control glasshouse: the whitefly population was reduced by 97.6 %. White pupae could not be detected at the final count on day 90 (Figure 2). The number of empty whitefly pupal cases increased from day 27 to day 42 from zero to about 10 per plant, and finally increased to 35 per plant on day 90 (Figure 2). During the first generation, the number of whitefly adults decreased from the day of release to almost zero on day 27. The number of whitefly adults of the second generation reached its top on day 42 with 4 per plant, and decreased to about 1.3 per plant on day 61. The number of adults of the third generation whiteflies reached an average of five per plant on day 68. The number of black pupae reached a level of 165 per plant on day 90 (Figure 2).

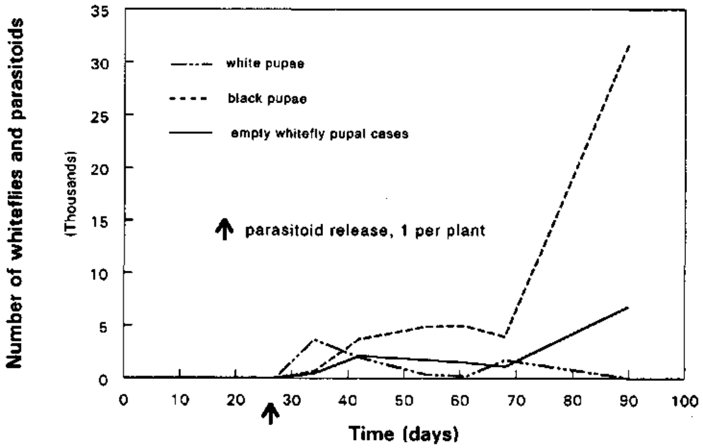

Figure 2. Population growth of *Trialeurodes vaporariorum* (white pupae and empty pupal cases) and *Encarsia formosa* (black pupae) on 192 *Gerbera jamesonii* plants during 90 days. One central release of 198 *E. formosa* was made on day 27.

In the glasshouse where on average three *E. formosa* per plant had been released, whitefly pupal cases increased only slightly and reached a level of 15 per plant at the final count. This is about a third of the number of empty pupal cases counted in the glasshouse where one parasitoid per plant had been released. The number of white pupae was less than one per plant at the final count (Figure 3). The adult whitefly population fluctuated in the same way as in the glasshouse where one *E. formosa* per plant had been released. The peak of the second generation was 8 per plant on day 44, and the peak of the third generation was 9 adults per plant. The final count on day 72 showed that the number of adults had decreased to less than 1 per plant. The number of black pupae increased to about 33 per plant on day 50, and eventually reached 44 black pupae per plant (Figure 3).

In both glasshouses where *E. formosa* had been released, the parasitoids found all whitefly infested plants. The total percentage parasitism increased from 58 % to 82 % in the glasshouse with one *E. formosa* per plant. In the glasshouse with release of three parasitoids per plant we found 82 % parasitism on day 56 and it remained high during the remainder of the experiment (Table 2).

Table 2. Percentage parasitism of *Trialeurodes vaporariorum* by *Encarsia formosa* in two glasshouses with different numbers of parasitoids released.

Day	% Parasitism 198 *E. formosa* released (1 parasitoid per plant; day 27)	 566 *E. formosa* released (3 parasitoid per plant; day 30)
0	-1)	-1)
21	0	0
27/28	0	0
34/35	57.7	0
42/44	63.5	67.9
50	no count	72.8
54/56	73.8	82.3
61/63	76.6	74.6
68	78.1	75.0
90	82.4	

1) = no whitefly pupal cases or black pupae present

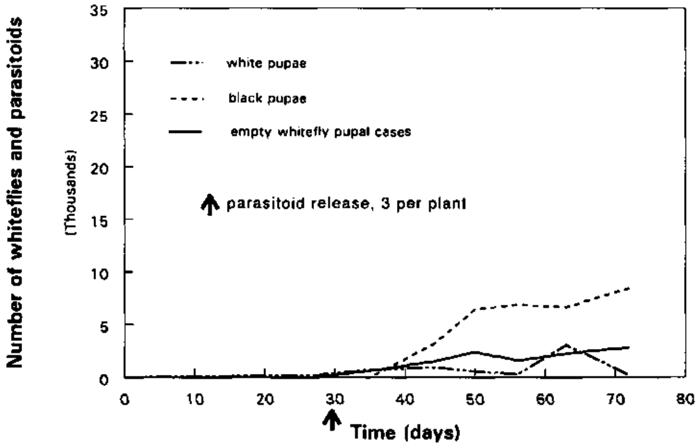

Figure 3. Population growth of *Trialeurodes vaporariorum* (white pupae and empty pupal cases) and *Encarsia formosa* (black pupae) on 192 *Gerbera jamesonii* plants during 72 days. One central release of 566 *E. formosa* was made on day 30.

DISCUSSION AND CONCLUSIONS

Dispersal

The dispersal pattern of the adult whitefly population was similar in the control glasshouse and the glasshouse where one *E. formosa* per plant had been released. The parasitoids did apparently not influence the dispersal pattern of whiteflies. The released whitefly adults dispersed mainly in the double middle row where they had been released. Adults of the second generation dispersed also to the neighbouring double rows and, therefore, over the whole glasshouse. Taylor and Taylor (1977) reported that greenhouse whiteflies do aggregate at low densities, but tend to disperse at high densities, and we observed the same. But dispersal may also have become easier in the course of our experiments, because the *Gerbera* canopy became very dense which facilitated crossing to the other rows. During the second generation whitefly adults were found on all plants. In the glasshouses where parasitoids were released, whiteflies were parasitized on all host-infested plant, and *E. formosa* dispersed throughout the glasshouse.

Population dynamics

Growth of an undisturbed whitefly population on *G. jamesonii* plants is exponential. Where on average one *E. formosa* per plant was released, a substantial smaller population of greenhouse whiteflies was found. Here, the increase in *T. vaporariorum* density was much slower compared to the the control glasshouse. However, at the end of this experiment the leaves of the plants were heavily covered with honeydew and sooty mould. The conclusion is that release of one *E. formosa* per plant is insufficient for good control.

One well timed central release of on average three parasitoids per plant reduced the whitefly population to a level more than a hundred times as low as in the control glasshouse and three times as low as in the glasshouse where one *E. formosa* per plant had been released. Honeydew and whitefly adults were seen only seldomly on the plants and sooty mould could not be detected, so this release resulted in sufficient control.

The percentage parasitism of whitefly on *G. jamesonii* in our experiments was higher than found for tomato by Eggenkamp-Rotteveel Mansveld et al. (1982 a and b) and achieved with less than half of the number of *Encarsia formosa* introduced per plant. The initial whitefly infestation density had been much lower in Eggenkamp-Rotteveel Mansveld's experiments (less than 5 % of the plants was infested, and the average number of whiteflies was only 0.008 white pupae per plant) than in our experiments (average of two whitefly adults per plant). However, our experiments were done in a much smaller glasshouse which may result in an easier location of whiteflies by the parasitoids. The only data about commercial application of *E. formosa* against whitefly in *Gerbera* are from Blümel (1992). In her experiments in two commercial glasshouses with about 500 plants each, parasitism maximally reached 90 % during a 36 week period. The mean percentages of parasitism were much lower, while a total number of about 50 parasitoids per plant was released (Blümel, 1992). Currently, Koppert Biological

Systems advises to release preventively 1.5 parasitoids per m^2 per week during a period of at least 5 weeks in commercial *Gerbera* crops, which is about 2 parasitoids per plant. If a whitefly infestation is observed it is advised to release 3 parasitoids per m^2 per week, also during at least 5 weeks, which is about 4 parasitoids per plant. This usually results in sufficient control and these numbers are within the range of what we released.

In the next phase of our resarch we will test the effect of glasshouse size and plant spacing on the control efficiency of the parasitoid with experiments in semi-commercial glasshouses and with a simulation model for *G. jamesonii, T. vaporariorum* and *E. formosa.* This model has earlier been used for obtaining insight in the relationship between the parasitoid and whitefly in a tomato crop (van Roermund et al., 1997).

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CHAPTER 8

INFLUENCE OF THE HOST PLANT *GERBERA* ON BIOLOGICAL CONTROL OF GREENHOUSE WHITEFLY WITH THE PARASITOID *ENCARSIA FORMOSA* IN GLASSHOUSES: EXPERIMENTS AND SIMULATION

SUBMITTED AS:
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INFLUENCE OF THE HOST PLANT *GERBERA JAMESONII* ON BIOLOGICAL CONTROL OF
TRIALEURODES VAPORARIORUM WITH THE PARASITOID *ENCARSIA FORMOSA* IN GLASSHOUSES:
EXPERIMENTS AND SIMULATION

INFLUENCE OF THE HOST PLANT *GERBERA* ON BIOLOGICAL CONTROL OF GREENHOUSE WHITEFLY WITH THE PARASITOID *ENCARSIA FORMOSA* IN GLASSHOUSES: EXPERIMENTS AND SIMULATION

ABSTRACT

Biological control of greenhouse whitefly, *Trialeurodes vaporariorum*, with the parasitoid *Encarsia formosa* was studied in glasshouses with *Gerbera jamesonii* plants. Possible causes for failure or success of biological control in this ornamental crop were identified. First, experiments in glasshouses were performed and subsequently these results obtained in glasshouses were further analysed by a simulation approach.

The simulated population increase of greenhouse whitefly in the absence or presence of the parasitoid agreed well with the observed data on *Gerbera* in small and large glasshouses. Simulation and observation data did not agree in an experiment where the introduced whiteflies were in a bad condition.

Possible causes for hampering biological control on *Gerbera* were studied. It was found that the rosette type plant architecture was not negatively influencing searching behaviour of the parasitoid. The leaf hairiness of *Gerbera* played only a small role in reduction of searching efficiency. The large total leaf area of a *Gerbera* crop had a slight negative effect on the number of hosts encountered by parasitoids. In our experiments, the release of a total of three parasitoids per plant was not sufficient for control of whitefly in *Gerbera* in the large glasshouse. *Gerbera* cultivar differences had a significant effect on fecundity and development of whitefly, resulting in different rates of whitefly population increase, which might make biological control more difficult on the least resistant cultivar. Of all the effects studied with the simulation model, glasshouse temperature was identified as the most important factor for success or failure of biological control. Average glasshouse temperatures in commercial *Gerbera* crops may be too low for successful biological control during the winter and spring period.

Biological control of whitefly on *Gerbera* can be improved by (1) a release strategy of at least four parasitoids per plant in five weekly intervals, (2) using more resistent *Gerbera* cultivars, and (3) increasing glasshouse temperature by two degrees early in the season.

INTRODUCTION

Biological control of whitefly is currently widely used in most glasshouse vegetable crops in the Netherlands and other countries with an important glasshouse industry (van Lenteren, 2000). Biological control of pests is also desirable in ornamentals, in order to reduce the abundant use of and dependence on pesticides (Gullino & Wardlow, 1999). In many European countries (Belgium Denmark, France, Germany, Italy, Sweden, The Netherlands, United Kingdom) the introduction of natural enemies has started during the last decade of the 20th century in commercial ornamental glasshouses (van Lenteren, 1996 and 1999; Wardlow & van Lenteren, 1993).

However, biological control in ornamentals appeared more difficult than in vegetables. There are various reasons for this, both biological and non-biological (Fransen, 1992). We have chosen the ornamental plant *Gerbera jamesonii* Hook as a model crop for development of biological control of whitefly, because (1) usually the leaves of this plant are not harvested and this allows the presence of low populations of the pest organisms in the crop as long as they do not damage the flowers, and (2) much is known of the biology of greenhouse whitefly and its natural enemy *Encarsia formosa* (e.g. van Lenteren & Martin, 1999).

Population dynamics of greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood), and its parasitoid *Encarsia formosa* Gahan have been extensively studied on laboratory, experimental glasshouse and commercial glasshouse scale on vegetable crops like tomato and cucumber (e.g. Eggenkamp-Rotteveel Mansveld et al., 1982a and 1982b; Noldus et al., 1985; Noldus et al., 1986; Martin et al., 1991; van Roermund, 1995; Xu Rumei, 1991). These experiments were the basis for successful biological control of the pest on these crops.

In laboratory research with *T. vaporariorum* and *E. formosa* on *G. jamesonii*, comparable results were found to those on vegetable crops concerning host location and foraging behaviour of the parasitoid (Sütterlin & van Lenteren, 1997, 1999, and 2000). This was unexpected because of the difference in plant architecture of *Gerbera,* which is of a rosette type, in contrast to vegetables such as tomato and cucumber, which are vertically orientated. The dispersal behaviour of whitefly on *G. jamesonii* is very much comparable on both plant types (tomato and *Gerbera*): a preference for the youngest leaves for feeding and oviposition by the whitefly adults was observed. Thus, the preferred host stages for oviposition by *E. formosa* are found on the fully grown leaves (van Lenteren & Martin, 1999, Noldus et al., 1986, Sütterlin et al., 1991, Xu Rumei, 1991). However, the parasitoid searches on leaves of all age classes of *G. jamesonii* plants. When allowed to fly to host plants from a short distance, the first landing of *E. formosa* is at random on uninfested and host infested *Gerbera* leaves (Sütterlin & van Lenteren, 2000). Nevertheless, a redistribution of parasitoids from uninfested towards infested leaves occurred over the course of 24 h, as the parasitoids are arrested on infested leaves after encounters with whitefly hosts (Sütterlin & van Lenteren, 2000).

Do these findings about the behaviour of *E. formosa* on *Gerbera* in the laboratory mean that successful biological control of *Gerbera* could be a realistic option in glasshouses? To answer this question, the step-wise approach from laboratory experiments to large glasshouses as suggested by Van Driesche & Bellows (1996) is used here. We initially performed experiments in small glasshouses (60 m^2). Successful biological control - that is a low whitefly population during the experimental period, very little honeydew, few whitefly adults on the leaves (about 0.5 adult per plant) and no development of sooty moulds - was achieved with one central release of on average three parasitoids per plant (Sütterlin et al., submitted).

Further experiments in larger glasshouses were designed to see if *E. formosa* reduces whitefly sufficiently at this scale. These experiments are described in this paper. The larger, semi-commercial glasshouse differs from the small glasshouses in the following respects: (1) Size of plants: larger number of leaves per plant due to the longer growing period of the crop. (In a commercial glasshouse, the crop is cultivated for two to three years, and eventually an average of 50 - 60 leaves per plant can be reached). (2) Parasitoid dispersal: parasitoids have to search over longer distances and on larger areas before finding hosts. (3) Population dynamics: more insect generations occur and pest control has to be achieved over a longer period.

To be able to integrate the results of these experiments on different scales, system analysis and simulation can be helpful tools, to gain insight in the multitude of relationships between the three trophic levels plant, herbivorous insect and parasitoid, and to derive most important factors that determine successful biological control. With this approach an integration of the most relevant processes can be obtained and the step from knowledge at the individual level towards understanding processes at the population level can be made. To explain the population dynamics of greenhouse whitefly and its parasitoid on *Gerbera*, the simulation model of van Roermund et al. (1997a) was adapted for this crop. The experimental results described in Sütterlin et al. (submitted) and in this paper (Experiment III) will be used to validate the simulation model for *Gerbera*.

With this model we (1) obtain insight in how *E. formosa* reduces whitefly populations in glasshouses on *Gerbera*, (2) may improve the introduction schemes for parasitoids in crops like *Gerbera*, where control was supposed to be more difficult to attain than in vegetables and (3) can predict effects of changes in cropping practices (e.g. greenhouse temperature, *Gerbera* cultivar) on the result of biological control.

MATERIAL & METHODS

Experiment I: Greenhouse whitefly fecundity and development time

In order to have some idea about the variation in quality of *G. jamesonii* cultivars for whitefly, and to be able to estimate its effects for biological control, whitefly development time and fecundity were measured on three cultivars. Gerbera cv.'s 'Fame' (112 trichomes per cm^2 leaf area), 'Macho' (80 trichomes per cm^2 leaf area) and 'Tennessee' (363 trichomes per cm^2 leaf area) were used. The fecundity of whitefly females was measured on young leaves of the plants. Whitefly females were taken randomly from a whitefly rearing on *Gerbera*, cv. 'Fame' and were one to seven days old. They were put into leaf cages on the leaves for 48 h, in three glasshouse compartments of 16-20 °C, 20 °C and 25 °C, respectively. Temperatures in the latter two compartments varied less than 0.25 °C. Number of whitefly eggs laid per female was measured at 48 h intervals.

The total whitefly egg to adult development time was measured using whitefly on young to medium old leaves of the three cultivars. The development of immature whitefly stages was checked once a day, until adults emerged. Two glasshouse compartments with constant temperatures of 20 °C and 25 °C were used during this experiment. The total development time of each immature stage was recorded and the 50 % development point of the population (or median) was determined. At the constant temperature of 25 °C, cv. 'Fame' was used in two independent experiments, in the results indicated as 'Fame' and 'Fame' (b).

Experiment II: Small glasshouses

Plants of cv. 'Tennessee', a 'hairy' cultivar (363 trichomes per cm^2 leaf area) was grown on rockwool in two glasshouses with 192 plants in each. Each plant had approximately twenty leaves. Automatic temperature (set point 20 °C) registration was used, and relative humidity (60 - 70 %) was measured. During the experimental period, the temperature was recorded every hour, and varied mostly between 20 - 25 °C with a few peaks at 30 - 33 °C. One glasshouse served as a 'control'. In this 'control', 362 whitefly adults (sex ratio 1:1) were released on four plants in the centre of the glasshouse. In the other glasshouse 375 whitefly adults (sex ratio 1:1) were released, and 27 days later 198 *E. formosa* adults were released centrally (= on average one parasitoid per plant). The experiment started on day 127 from 1 January and lasted 84 (control) and 90 (parasitoid release) days, respectively.

The data of this experiment (Sütterlin et al., submitted) will be used for validation of the simulation model (see later section).

Experiment III: Large glasshouse

Eighteen hundred plants of cv. 'Tennessee' with approximately 40 leaves per plant were grown on rockwool in 18 rows of 100 plants each in a 300 m^2 glasshouse. The experiment started on 25 February (day 56 from 1 January) and lasted 98 days (until 3 June, day 154). The temperature was recorded every hour. The minimum temperature was set at 17 °C, and the temperature did generally not increase above 25 °C, with very few peaks around 30 °C (Figure 1).

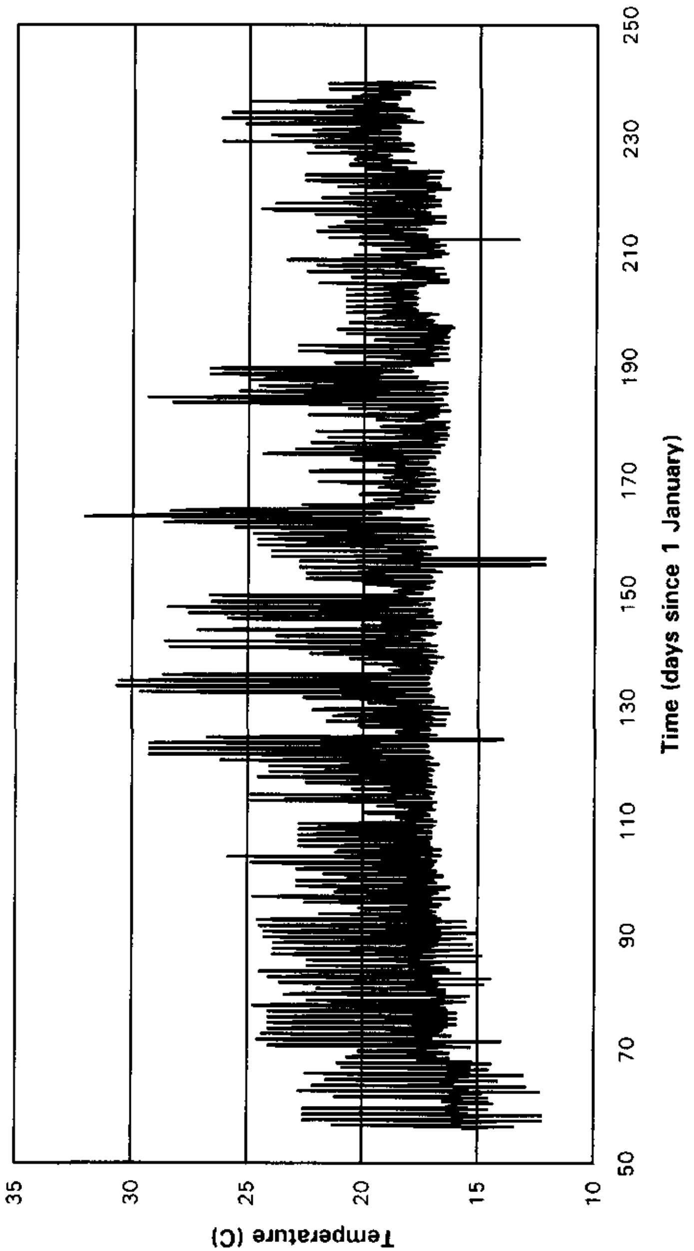

Figure 1. Hourly temperatures in a large glasshouse over 185 days (Experiment III).

First phase of experiment. Adults from a whitefly rearing on *Gerbera* (Sütterlin & van Lenteren, 1999) were introduced on day 56 of the experiment in 6 clusters of 4 plants, distributed throughout the glasshouse. On each of the 24 whitefly 'introduction' plants, 50 adults were released, so a total of 1200 whitefly adults were introduced in the glasshouse with a sex ratio of 1:1. After the day of release, 224 whiteflies were found dead and the other 976 were assumed to be alive in the crop canopy. Three weeks after whitefly introduction, on days 77, 84 and 91 (18 and 25 March, 1 April) *E. formosa* were released, with a total of 1800 pupae on 30 paper cards per release (i.e. one parasitoid per plant per release), uniformly distributed over the glasshouse. This release method is comparable with the commercial method for introducing parasitoids on *Gerbera* in the first half of the 1990s (pers.com. Koppert Biological Systems, Berkel en Rodenrijs, The Netherlands). The number of whitefly adults was counted on all leaves of all plants on days 75, 82, 96, 111 and 154.

Second phase of experiment. Eighty-nine days after the start of the experiment, the whitefly population was almost extinct, and a second release of whiteflies was made on 4 June (= day 155) and population development was studied over a period of 85 days. A check of all plants and leaves yielded a number of 616 adults still in the canopy on 3 June. A total of 600 extra adults were then introduced in six clusters of two plants on 4 June. One day later, 30 whitefly adults were found dead, 570 were assumed to be alive in the canopy, together with the 616 whitefly adults from the previous experimental phase. So, a total of 1186 whiteflies were present, approximately the same as during the first phase of the experiment. On days 167, 188 and 210 (16 June, 7 and 29 July) parasitoids were introduced on paper cards uniformly distributed over the glasshouse: 0.5, 1 and 0.5 parasitoids per plant, respectively.

During the second phase of the experiment the number of whitefly adults was counted on days 159, 166, 187, 202, 229 and 236.

THE SIMULATION MODEL

The model is individual-based and simulates the local searching and oviposition behaviour of individual parasitoids in a whitefly-infested crop. The model includes stochasticity and spatial structure, and comprises several submodels for (a) the parasitoid's foraging behaviour, (b) the whitefly and parasitoid population development, (c) the spatial distribution of whitefly and parasitoid within and between plants in the crop, and (d) leaf production. The population dynamics of whitefly and parasitoid are linked through simulation of the foraging behaviour of individual parasitoids on leaves in the crop. The model uses a mechanistic behavioural basis for the ecological processes and incorporates more biological detail (i.e. behaviour of individuals) than most other models of insect-parasitoid interaction (e.g. Barlow, 1999). A simplified scheme of the model is given in Figure 2 (after Van Roermund et al. (1997a)).

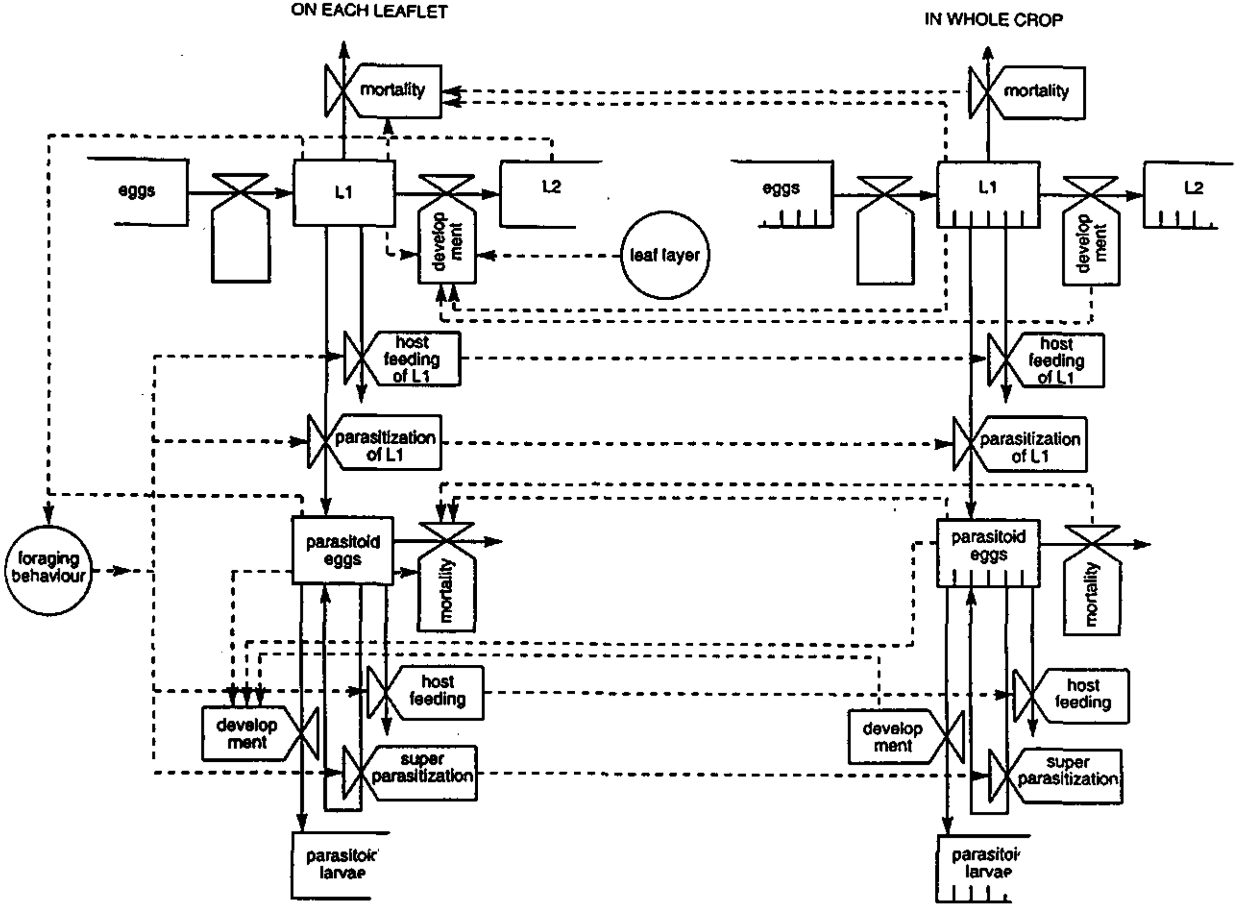

Figure 2. Relational diagram of the simulation model for the population growth of the greenhouse whitefly and *E. formosa*, with details o the interaction between host and parasitoid. The state variables or integrals (insect numbers) are presented within rectangles, the rates of change within valve symbols, and auxiliary variables within circles. The flow of material is presented by solid arrows and the flow of information by dotted arrows. Small bars in a rectangle indicate a series of integrals (boxcar train) (after van Roermund et al., 1997a).

For a comprehensive description of the model, see Van Roermund et al. (1997a). Five identical input runs were simulated because of the stochasticity of the model.

Model adaptation for *Gerbera*

In the study concerning tomato, it was concluded that the degree of whitefly control by *E. formosa* was sensitive to several model input-parameters, such as giving up times (GUT= time from last host encounter on the leaf until flying away from the leaf) and walking behaviour of the parasitoid, whitefly development duration and also total leaf area in the crop (van Roermund et al., 1997a). The following parameters have different values for *Gerbera* and tomato (Table 1): (1) the GUT of the parasitoid after each host encounter (2) the walking speed and (3) walking activity of the parasitoid, (4) the GUT on each leaf side (resulting in a certain ratio of search time on both leaf sides), (5) the whitefly development duration, and (6) total leaf area: number, size and development of new leaves in the crop. The input parameters for the simulation study given in Table 1 were obtained from data published by our group.

Table 1. Data on foraging parameters of *E. formosa* on *Gerbera* leaves (Sütterlin & van Lenteren, 1997, 1999 and 2000) and tomato leaflets (van Roermund & van Lenteren, 1995).

Foraging parameter	*Gerbera*	Tomato
Walking speed (cm/min), 20 °C	1.50	1.86
Walking activity*, 20 °C	0.60	0.75
Probability of landing on lower leaf side	0.75	0.50
% time spent on leaf side of introduction on clean leaf(let)	100.0	64.5
Giving up time (GUT) on clean leaf (let) (min)	83	20
Increase of GUT, when honeydew is on the leaf(let)	Assumed 5x	5x
Increase of GUT after oviposition in unparasitized host	Assumed 2x	2x

* Fraction of time spent walking on a clean leaf(let)

Foraging behaviour of the parasitoid

When developing a realistic model based on behaviour of individual parasitoids, information is needed on the time allocated to searching for and oviposition in hosts by the parasitoids on leaves. In addition, information on the parasitoid's walking speed, walking activity and host-handling behaviour on leaves is needed. The need for information about these parameters was made clear by van Roermund et al. (1997a), after evaluating the influence of approximately 24 parameters in a sensitivity analysis on the results of biological control. From research done earlier in our group (van Lenteren et al., 1996; van Roermund & van Lenteren, 1995; Sütterlin & van Lenteren, 1999), the following conclusions can be drawn. *E. formosa* searches at random on leaves. Parasitoids are arrested on the leaf by encounters with, and especially by ovipositions in unparasitized hosts, by encounters with parasitized hosts and by contact with honeydew. The average residence time on clean *Gerbera* leaves was found to be 83 min ± 59 *SD* (Sütterlin & van Lenteren, 1999). The giving up time (GUT) on infested *Gerbera* leaves is about 36 min ± 8 *SD*. However, many parasitoids did not leave the leaf before the end of the experimental period, which means that their GUT could not be observed and far exceeded 36 min.

The 'patch leaving behaviour' of *E. formosa* can be described by a stochastic threshold mechanism, which is characterized by a certain tendency (probability per unit of time) to leave the leaf (Kalbfleisch & Prentice, 1980; Bressers et al., 1991). For a detailed description of the submodel of foraging behaviour of *E. formosa*, see van Roermund et al. (1996 and 1997b).

Life history parameters of whitefly and parasitoid

Life history data for greenhouse whitefly and *E. formosa* are input for the model and can be found for tomato in van Roermund & van Lenteren (1992a and b). For *E. formosa*, the life history parameters appeared not to be dependent of host plant species or cultivar, so these data do not differ between *Gerbera* and tomato. Data of van Roermund & van Lenteren, (1992b) were used in the model.

Life history data of whitefly on *G. jamesonii* can be found in Sütterlin & van Lenteren (submitted). These data are summarized in Table 2, and were supplied in a later phase of the simulation study with new data from Experiment I presented in this paper (see Results: Table 4 and 5).

Table 2. Important life history parameters of *T. vaporariorum* on *G. jamesonii* (Sütterlin & van Lenteren, submitted) and tomato (van Roermund & van Lenteren, 1992 (a))

Parameter	*Gerbera*	Tomato
Total development time egg – adult (days), 20 °C	37.5	31.8
% mortality egg to adult, 25 °C	55.9	16.7
Longevity adult females (days), 20 °C	51.4	41.4
Total fecundity (eggs/female), 20 °C	278	163

Leaf production during crop growth

An important parameter for crop growth is the leaf initiation rate (LIR, in leaves per day), that is the reciprocal of the time necessary for the plant to produce a new leaf. LIR is also needed as an input parameter for the model.

The influence of temperature and light intensity on the LIR of *Gerbera* is described by Leffring (1981). A clear temperature effect was found between 15.7 and 23.7 °C. The average LIR at these temperatures were 0.082 leaf/day (± 0.007 *SD*) and 0.112 leaf/day (± 0.012 *SD*), respectively. Thus, it takes between 8.9 and 12.2 days until a new leaf is produced by a *Gerbera* plant. In the model here, it was assumed that the maximum LIR was reached at 23.7 °C and that the rate increased linearly between 15.7 and 23.7 °C. Data for *G. jamesonii* and tomato are summarized in Table 3.

Table 3. Leaf production, surface and number for *G. jamesonii* (Leffring, 1981, and Sütterlin, unpublished) and tomato leaves (van Roermund & van Lenteren, 1995).

Parameter	*Gerbera*	Tomato
Leaf initiation rate (leaves per day), 20 °C	0.098	0.43
Average leaf size (cm^2)	224	154[1)]
Max. number of leaves per plant	50	20

[1)] One leaf consists of seven leaflets

Model initialization

The model is initialized by introduction of a certain number of adult whiteflies and parasitoids in the crop. Number of plants, initial number of leaves per plant and initial insect numbers, their location in the canopy and dates of releases of whiteflies and parasitoids are defined. Variable, actual temperature and light period for each day are the driving variables.

The model was validated with the data from population counts of whiteflies and parasitoids of experiment II and III.

RESULTS

Whitefly fecundity and development duration (Experiment I)

Whitefly fecundity and duration of development have been determined for three *Gerbera* cultivars (Table 4 and 5). The fecundity was temperature dependent and for all three cultivars highest at the highest temperature (25 °C; cv. 'Tennessee', Kruskal-Wallis test, $P << 0.001$; cv. 'Macho', Kruskal-Wallis test, $P << 0.001$ and cv. 'Fame', Kolmogorov - Smirnov test, $P = 0.005$). At 25 °C, the number of eggs laid per female during 48 h was significantly higher on cv. 'Tennessee' than on cv. 'Macho' (Table 4). This difference can also be seen between cv. 'Fame' and cv. 'Macho', but was not significant (Kolmogorov - Smirnov, $\alpha= 0.017$ after Bonferroni correction, $P = 0.019$). At a temperature of 16 - 20 °C, a difference between cultivars 'Tennessee' and 'Macho' can be seen, but was also not significant (Kolmogorov - Smirnov test, $P = 0.060$).

The total development time of greenhouse whitefly was also dependent on temperature and differed between cultivars (Kruskal-Wallis, $P_{20°C}=0.012$ and $P_{25°C}<0.001$, followed by pair-wise comparison, Table 5), but not in the same way as fecundity did. On cv. 'Macho' the total whitefly development time was longest at both constant temperatures, and on cv. 'Fame' it was shortest. The lowest performance of greenhouse whitefly, i.e. a low fecundity and long development time, was found on cv. 'Macho' for both life-history parameters.

Table 4. Fecundity (eggs/female/48h) of *Trialeurodes vaporariorum* on three *Gerbera jamesonii* cultivars, 'Macho', 'Tennessee', 'Fame' at two constant (20 and 25 °C) and a fluctuating temperature (16-20 °C).

	Fecundity (eggs/female/48h)								
Temperature	16-20 °C			20 °C			25 °C		
	Mean	±*SD*	n	Mean	±*SD*	N	Mean	±*SD*	N
Cv. Macho	4.3a	1.8	56	11.7b	3.2	17	19.4c	4.1	42
Cv. Tennessee	6.0a	1.8	76	15.6b	4.4	17	36.2d	9.9	35
Cv. Fame	-	-	-	12.0b	2.5	16	27.9cd	6.9	40

Different letters within a row, indicate significant differences between the fecundity at different temperatures (Kruskal-Wallis, $P_{Macho} << 0.001$ and $P_{Tennessee} << 0.001$; Kolmogorov-Smirnov, $P_{Fame} = 0.005$). Different letters within a column, indicate significant differences between fecundity on different cultivars (Kruskal-Wallis $P<<0.001$, followed by a multiple comparison after Bonferroni correction of α).

Table 5. Total development time (egg - adult) of *Trialeurodes vaporariorum* on three *Gerbera jamesonii* cultivars at constant temperatures of 20 and 25 °C.

	Temperature					
	20 °C			25 °C		
	Total development time in days					
Cultivar	Mean ± SD	Median	n	Mean ± SD	Median	n
'Macho'	41.0 ± 2.3	40.0	18	29.8 ± 3.4	29.1	235
'Tennessee'	39.5 ± 3.7	38.9	58	27.5 ± 2.9	27.6	159
'Fame'	37.9 ± 1.8	36.4	13	26.6 ± 2.2	25.8	186
'Fame' (b)	-	-	-	23.1 ± 1.2	22.8	118

Validation of whitefly population growth

The observed (Experiment II, small glasshouse) and simulated development of whitefly populations in the absence of parasitoids is shown in Figure 3. Time is given as day number from 1 January. During the first four weeks (day 125 - 155) the number of adult whiteflies decreased steadily, because whiteflies were introduced as adults only. After that period, which coincides with the emergence of the second generation of whitefly adults, the population increased rapidly. A distinct third generation is not visible, because the whitefly generations are already overlapping by that time. By the end of the experiment, the number of adults reached a very high level of on average 48 per plant.

The result of one simulation is presented, because the five simulation runs were almost identical. The simulated curve agrees well with the observed population counts, both qualitatively and quantitatively. This result can be explained by the accurate estimates of the 'life-history' parameters of the greenhouse whitefly on *Gerbera*, used as input in the model. These were estimated from independent experiments described in Sütterlin & van Lenteren (submitted) and determined from data in Table 4 and 5.

Validation of combined whitefly and parasitoid population growth

Experiment II: Small glasshouse

With the release of one parasitoid per plant the whitefly population level was much lower than in the control situation (Figure 4). Whitefly adults also decreased during the first few weeks because only adults were introduced, after which an increase was observed. Two counts around day 185 yielded relatively low numbers of whitefly adults in the canopy, but shortly thereafter on day 194 a large number of adults was observed.

The simulated population of whitefly adults also decreased during the first few weeks, and then increased at the same time as the observed population (day 155 to 170), and reached a peak somewhat higher than the observed population counts: seven versus five adults per plant, respectively. The observed population counts showed the same pattern as the simulation did. However, differences are not large (note the linear scale of the y-axis) and population counts were based on only one experiment. Differences between replicates by a factor of two over 100 days are common in population studies when initiated with relatively few adults, as shown by replicate simulations of the whitefly population in van Roermund et al. (1997a). So, biological control was successful here, according to both the experiment and to the simulation. The observed number of black pupae (parasitised whiteflies) in the experiment increased from day 162 to 170 and then remained relatively constant for some 40 days. This was also simulated by the model (Figure 5). Only the observed number of black pupae at the end of the experiment was much higher than according to the simulation. This can be the result of our counts being composed of black pupae and empty black scales, while the simulation only accounts for black pupae and not the empty scales, which accumulate to high numbers on the leaves at the end of the experiment.

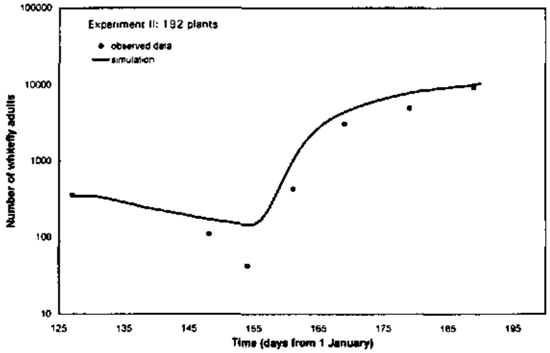

Figure 3. Observed and simulated number of adult whitefly in Experiment II in a small glasshouse, where 362 adults were released centrally on 4 plants. No release of parasitoids.

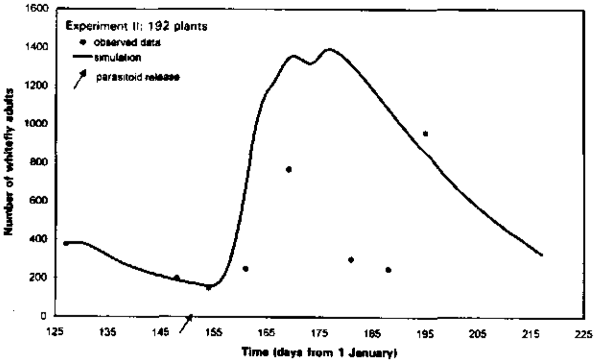

Figure 4. Observed and simulated number of adult whitefly in Experiment II in a small glasshouse, when the parasitoid *E. formosa* was released. 375 Adult whiteflies were released centrally on 4 plants and after 27 days (see arrow) 198 parasitoids were released centrally.

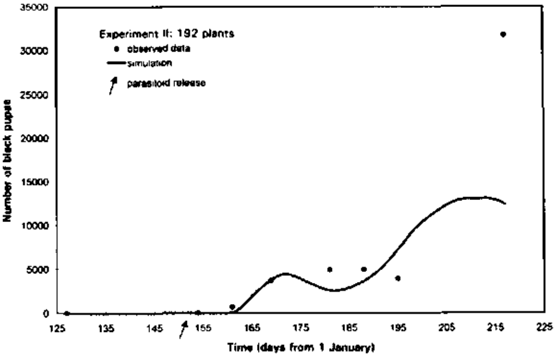

Figure 5. Observed and simulated number of black pupae in Experiment II. 375 Adult whiteflies were released centrally on 4 plants and after 27 days (see arrow) 198 parasitoids were released centrally.

Experiment III: Large glasshouse

First phase: The results of Experiment III (98 days) and the simulation results are presented in Figure 6. The number of observed whitefly adults in the glasshouse experiment was low and never above 0.4 adults per plant. From the initially released 1200 whitefly adults in the experiment, 18.6 % were found dead after the day of release, so the fitness of the whiteflies was probably suboptimal. During the experiment an unexpected whitefly mortality factor was observed: many whitefly immatures showed fungus (*Verticillium* spp.) infection.

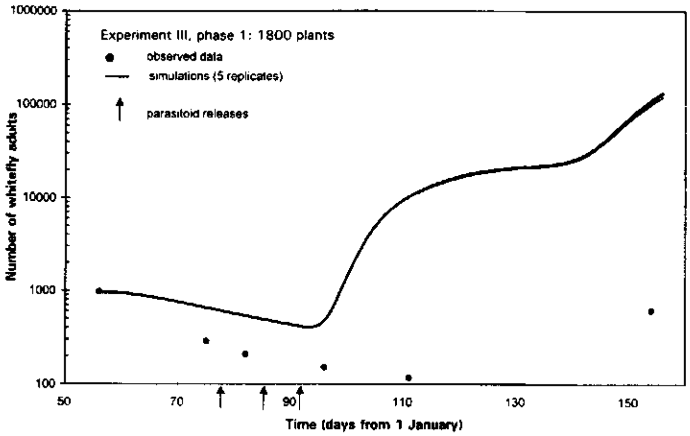

Figure 6. Observed and simulated (five replicates) number of adult greenhouse whitefly in Experiment III during the first phase, in a large glasshouse, when the parasitoid *E. formosa* was released. 976 adult whiteflies were released in six clusters of four plants each and on days 77, 84 and 91 (see arrows) about one parasitoid per plant was released, uniformly distributed in the canopy.

The simulation results show an enormous increase in the number of whitefly adults to a level of 56 adults per plant. After an initial decrease of adult numbers, a sharp increase was simulated around day 95, as was simulated and observed in the small glasshouse (Experiment II), when no parasitoids had been introduced (Figure 4). So, according to the model, the parasitoid introduction was not sufficient to control the whitefly population successfully. The low quality of the introduced whiteflies, plus the extra mortality of immatures by the fungus may have caused the low whitefly population in the glasshouse. Confirmation of this explanation was found from the results of the second experimental phase in the large glasshouse.

Second phase: a sharp increase in number of whitefly adults was observed here from day 188 to day 202, so the number of parasitoids introduced was not sufficient to control the whitefly population (Figure 7). The released whitefly adults survived much better during the first day (95 %) compared to those released in the first phase and no fungus infection was observed here during the course of the experiment. In the simulations the same increase in the number of whitefly adults is observed. In the first 33 days (day 155 to 188) we see a somewhat higher level of *T. vaporariorum* adults in the experiment compared to the simulations. This might be caused by the model assumption that no whitefly larvae and pupae were present in the glasshouse when the second whitefly adult introduction took place, whereas the 616 adults from the previous phase are expected to have produced some eggs and larvae. The number of adult whiteflies does not vary much between the five different simulation runs of the first phase (Figure 6) and the second phase of this experiment (Figure 7).

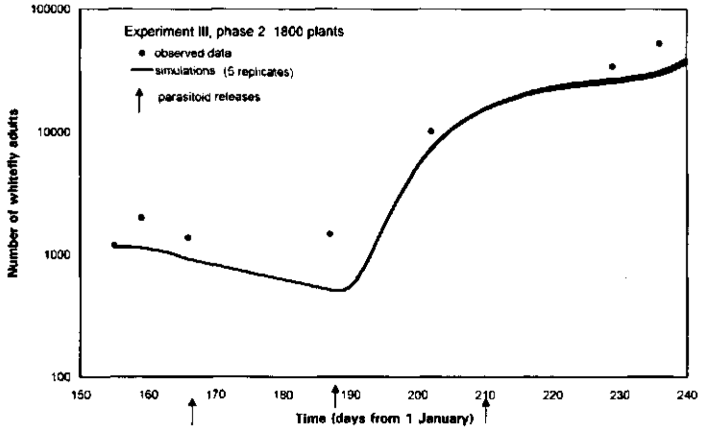

Figure 7. Observed and simulated (five replicates) number of adult greenhouse whitefly in Experiment III during the second phase, in a large glasshouse, when the parasitoid *E. formosa* was released. 1186 Adult whiteflies were present initially in the canopy and after 12, 33 and 55 days (see arrows) about 1, 0.5 and 1 parasitoid per plant was released, uniformly distributed in the canopy.

Figure 8a shows the simulated number of unparasitized whitefly pupae plus prepupae (white pupae). The simulation data cannot be compared to observation data, because only adult whiteflies were counted during the experiments. The five simulation runs are very similar. The simulation runs for the number of adult parasitoids (Figure 8b) vary little until day 211, and only after the last parasitoid 'introductions' differences occur.

Figure 9 shows the simulated percentage leaves infested with whitefly in the canopy and the percentage of parasitoids on whitefly-infested leaves. The simulation shows a steady increase in the percentage of leaves infested with whiteflies, but not more than 5 % of the leaves in the canopy is infested at the end of the 'experiment'. Just after the first release of *E. formosa* only a very low percentage of these parasitoids are searching on the whitefly-infested leaves, but this percentage increases during the course of the simulation to more than 40 %, because of the increase of giving up times of the parasitoids after encountering honeydew and/or whitefly immatures.

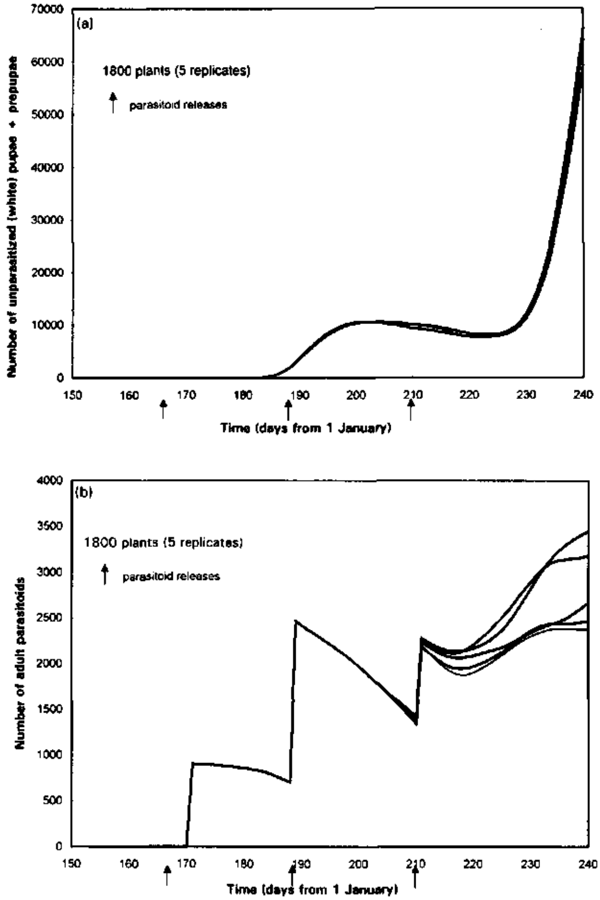

Figure 8. Simulation results (five replicates) during the second phase of Experiment III, with release of the parasitoid *E. formosa*. (a) Number of unparasitized pupae + prepupae (white pupae). (b) Number of adult parasitoids. Arrows indicate the release of parasitoids.

DISCUSSION

The aim of this study was to find out whether *E. formosa* can control whitefly populations in the crop *G. jamesonii*, and if not, to identify possible causes for failure. Biological control of greenhouse whitefly with the parasitoid

E. formosa was successful on *Gerbera* in small glasshouses as described in Sütterlin et al. (submitted) and in the small glasshouse of Experiment II, but not in the large glasshouse during the second phase (Experiment III). The potential causes for failure of biological control in the large glasshouse were identified with a simulation model.

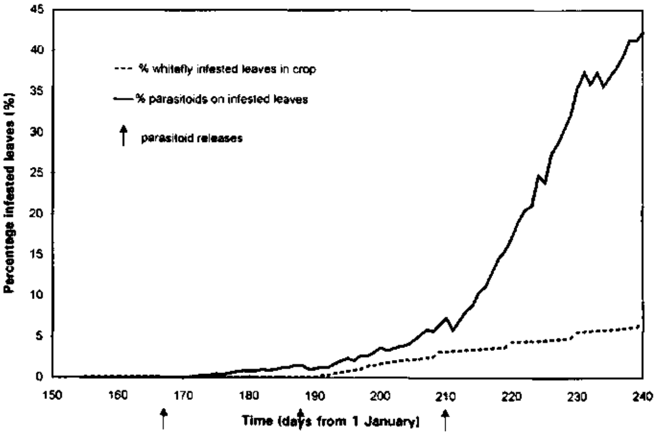

Figure 9. Simulation of the percentage whitefly infested leaves in the canopy and the percentage parasitoids on whitefly infested leaves during the second phase of Experiment III. Arrows indicate the release of parasitoids.

Simulation models and biological control

Many types of models have been developed for biological control systems. Berryman (1999) and Briggs et al. (1999) review the historical development of general models, focusing on discrete-time and continous-time models, which resulted in an enormous increase in ecological theory related to biological control. The most common complaint about theory is that it is too general and vague to be applicable to real biological control systems. The use of specific models in biological control is reviewed by Barlow (1999), who gives an overview of 50 such models. These models can be used in particular real-world systems or to very specific questions about such systems. We used a specific model, because we were interested in specific questions about whitefly control on *Gerbera* in comparison with that on tomato. With such a model, knowledge gained at the individual level in laboratory experiments can be integrated and then used for extrapolation to the population level in large glasshouses.

The simulated population increase of greenhouse whitefly in the absence of parasitoids agreed well with observations on *G. jamesonii*. This result can be explained by the accurate estimates of the life history parameters of the pest insect for this crop. In the presence of *E. formosa*, the simulation results agreed reasonably well with the observations in the small glasshouse. Timing and pattern of the population increase of whitefly adults and black pupae were simulated accurately.

Simulation of the first period of approximately 100 days in a larger glasshouse was not very accurate, except for the first 40 days. However, the fitness of the introduced whiteflies in the experiment is questionable, because almost 20 % were dead one day after release. Also, an extra mortality factor for the whiteflies was observed from day 90, as many immatures were found dead and overgrown by a fungus. The simulation model assumes healthy whitefly adults at the start of the experiment and no other mortality factors except *E. formosa*.

The simulated population increase of greenhouse whitefly in presence of its parasitoid agreed well with the observations during the second phase in the large glasshouse, when no fungus infestation was detected.

Comparison between Gerbera and tomato

Biological control of greenhouse whitefly with E. formosa is known to be very successful in tomato. Walking speed and walking activity of E. formosa are somewhat lower on Gerbera leaves compared to tomato leaves. Whitefly females live longer and produce more eggs on Gerbera, but development time is longer and immature mortality is much higher on this crop. Leaf initiation rate in the crop is much lower, but there is a larger area per leaf to be searched by the parasitoids, compared to tomato. Giving up times of E. formosa on Gerbera leaves are much higher than on tomato leaves. Because some of the differences between Gerbera and tomato favour biological control on Gerbera and some do not, a satisfactory explanation why biological control of whitefly in G. jamesonii is successful or not, is still to be given. By using the simulation model, where all these processes are integrated, such explanations can be found.

Possible explanations for the failure of biological control

(1) Release strategy: a too low number of parasitoids was introduced.

(2) Initial whitefly density: either too many or too few whiteflies were present at the start of the experiment.

(3) Parasitoid walking behaviour: because of the trichomes on *Gerbera* leaves, parasitoids walked too slowly and, therefore, encountered few hosts.

(4) Total leaf area of the crop: the total leaf area of the canopy during the second phase (Experiment III) was too large for the parasitoids to find whitefly.

(5) Cultivar effects: *G. jamesonii* cultivar caused a whitefly population-increase rate that was too high for the parasitoid or certain cultivar characteristics hampered parasitoid searching.

(6) Glasshouse temperature: differences in success of biological control between Experiment II and III were caused by differences in glasshouse temperature.

(1) Release strategy

The control strategy during Experiment III was a release of one *E. formosa* per plant, three times in week numbers 3, 4 and 5 (strategy 1). The simulation results of the large glasshouse (Experiment III) showed a large increase in the whitefly population (Figures 6 and 7). According to the model, the released number of parasitoids (strategy 1) could not control the *T. vaporariorum* population. In the small glasshouse (Experiment II), a total release of one parasitoid per plant was sufficient for successful control. Several release strategies have been evaluated with the simulation model during a 100-day-period to find out if the number and timing of parasitoid release could be improved to achieve successful biological control in this experiment (Table 6).

Five parasitoid releases at weekly intervals, beginning the third week after whitefly introduction is the best strategy according to the model (strategy 11, with most released parasitoids per plant i.e. 25). However, even this strategy does not lead to very low numbers of greenhouse whitefly in the large glasshouse and is therefore not successful. Comparing strategy 4 with 5, and strategy 6 with 7, it can be concluded from Table 6 that releasing a larger number of parasitoids at an early stage of the growing season is slightly better than dividing the number of parasitoids over a longer period of time in more releases.

Table 6. Effect of different release strategies of *Encarsia formosa* on the whitefly population. Cumulative number of unparasitized prepupae + pupae (white pupae) as percentage of that of strategy 1 (release of parasitoids three times in week number 3, 4 and 5 after whitefly introduction, at a rate of 1 parasitoid per plant each) and the final number of whitefly adults per plant after 100 days, as simulated by the model.

Strategy	Number of releases	Week number of releases	Number of parasitoids/ plant/release	Total number of released parasitoids/plant	% white pupae compared to strategy 1	Number of adults/plant, after 100 days
1	3	3, 4, 5	1	3	100.0	74
2	4	3, 4, 5, 6	1	4	91.0	67
3	5	3, 4, 5, 6, 7	1	5	86.5	63
4	6	3, 4, 5, 6, 7, 8	1	6	86.8	62
5	3	3, 4, 5	2	6	81.5	58
6	6	3, 4, 5, 6, 7, 8	2	12	64.3	44
7	3	3, 4, 5	4	12	51.9	35
8	4	3, 4, 5, 6	4	16	43.7	29
9	4	2, 3, 4, 5	4	16	44.0	29
10	5	3, 4, 5, 6, 7	4	20	40.4	26
11	5	3, 4, 5, 6, 7	5	25	29.5	18

(2) Initial whitefly density

Initial whitefly density can be of importance for the numerical response of the parasitoid. The initial numbers released in the large glasshouse (Experiment III, both experimental phases) were 0.5 to 0.6 adults per plant, while the initial density in the small glasshouse (Experiment II) was two adults per plant. In another glasshouse with successful biological control also two whitefly adults per plant were initially released (Sütterlin et al., submitted). So, biological control was successful in *Gerbera* with the higher initial whitefly density. This larger whitefly population can cause a high numerical response of the parasitoid and thus has a positive effect on the biological control, as is shown in this study (see later: effect higher temperature).

(3) Walking behaviour of the parasitoid

Differences in leaf hairiness of *Gerbera* plants lead to a lower walking activity and walking speed of the parasitoid, when compared with the data for tomato (Sütterlin & van Lenteren, 1997). Adapting the walking speed and walking activity of *E. formosa* with the ones observed on tomato, changed the simulations only slightly. Table 7 shows a reduction of the whitefly population of only 9.4 %, so the lower walking speed and walking activity of the parasitoid have only a minor effect on the control level obtained in Experiment III.

Earlier work has shown that leaf hairiness negatively influences the foraging behaviour of natural enemies: for *E. formosa* on cucumber cultivars (van Lenteren et al., 1995), for four different *Encarsia* species and a coccinelid predator on Poinsettia cultivars (Heinz & Parella, 1994), for the predatory mite *Phytoseiulus persimilis* on *Gerbera* cultivars (Krips et al., 1999) and for *Trichogramma exiguum* on three different plant species (Keller, 1987). To our surprise, leaf hairiness does not seem to have a very negative influence on searching by *E. formosa* on *Gerbera*, as became clear after experiments at laboratory scale (Sütterlin & van Lenteren, 1997 and 1999) and simulations on a glasshouse scale (this study).

(4) Leaf area of the crop

The leaf area index (LAI) of *Gerbera* was high at the end of the second phase in the large glasshouse (Experiment III): 4.7 m^2 leaf area per m^2 soil. As *E. formosa* searches on both sides of a leaf, the leaf area for the parasitoid is 9.4 m^2. During the first phase of the experiment there were about 40 leaves per *Gerbera* plant, whereas in the small glasshouse the plants had on average 20 leaves at the start (Experiment II). The difference in leaf number and area might be the cause of control failure, because random search of *E. formosa* on all leaves decreases the encounter probability with hosts. For comparison, the LAI of a tomato crop has a peak in late spring of 3 m^2 leaf area per m^2 soil. If the initial number of leaves of a *Gerbera* plant was reduced by 50 %, a reduction of the whitefly population of 26 % was simulated (Table 7). The resulting whitefly population (52 adults per plant on day 100) is still too high for successful biological control, and thus, the difference in the number of leaves per plant and total leaf area only partly explains the difference in control between the small glasshouse (Experiment II) and the large glasshouse during the second phase (Experiment III).

In the model it is assumed that *E. formosa* searches all leaves, host-infested or not. The strong effect of leaf area on the number of *E. formosa* host encounters on tomato leaves, that resulted in a lower whitefly population on the tomato crop (van Roermund et al., 1997c), was less obvious in a *Gerbera* crop. Effect of leaf area on parasitoid host encounters was studied for *Trichogramma brassica* searching for *Ostrinia nubilalis* on maize plants and also in this case the parasitoid was less hampered than expected from the large leaf size of maize (Suverkropp, 1997). In *E. formosa*, the percentage of adult parasitoids on host-infested leaves increases as a consequence of the increase in GUT after host- or honeydew encounters (arrestment effect, see van Roermund & van Lenteren, 1995 and Sütterlin & van Lenteren, 1999).

(5) Cultivar effects

Development time of whiteflies and to a lesser extent fecundity are important parameters for the whitefly population development, according to the sensitivity analysis of the model (Van Roermund & van Lenteren, 1997(a)). This study showed that differences between life history parameters of *T. vaporariorum* on different *Gerbera* cultivars exist, while it was argued before that performance of the greenhouse whitefly was not influenced by different *G. jamesonii* cultivars (Dorsman & van de Vrie, 1987 and unpublished). These differences in life-history parameters of *T. vaporariorum* (Tables 4 and 5, and Sütterlin & van Lenteren, submitted) for different *Gerbera* cultivars could be the cause of differences in development of the whitefly population. The development time on cv. 'Macho' is 7.5 % longer than the average of three cultivars (cv.'s 'Fame', 'Macho' and 'Tennessee') which has been used in the model, both at 20 and 25 °C. The greenhouse whitefly fecundity on cv. 'Macho' is 14 % lower than the average of the three cultivars at 20 °C (Table 4 and 5). The longer development time and lower fecundity of cv. 'Macho' led to a 50 % lower whitefly population on this cultivar after 100 days compared to the previous simulated population (Table 7). Although this is a considerable reduction of the whitefly population, the simulated level of 30 adults per plant after 100 days is still too high and would be regarded as insufficient control. So, cultivar differences do not fully explain the failure of biological control in the larger glasshouse.

Krips et al. (1998) found similar differences in development of the spider mite *Tetranychus urticae* on different *Gerbera* cultivars.

(6) Glasshouse temperature

In a glasshouse where biological control of whitefly was successful (Sütterlin et al., submitted), the average temperature was approximately two degrees higher than in the glasshouse of Experiment III where control was insufficient. In experiment III, the lowest temperature was set at 20 °C (Sütterlin et al., submitted), just as in Experiment II where biological control was also successful. In the large glasshouse (Experiment III) of this study the temperature regularly fell to much lower temperatures, such as 16 and 17 °C (Figure 1). To evaluate the effect of temperature on biological control the glasshouse temperature of Experiment III was 'increased' in the model by 2 °C during the whole period. This temperature increase resulted in a reduction of the whitefly population by 55 % compared to Experiment III (Table 7). But more important, the peak whitefly population at the end of the experiment was drastically reduced from 73 to 16 adults per plant (Figure 10a). From day 140 onwards differences become very clear. A strong impact on the parasitoid population is also seen (Figure 10 b). The number of adult parasitoids increases exponentially, while the number in Experiment III remained low. The increase of 2 °C in the model reduced the development duration of whiteflies by five days and a larger whitefly population is simulated between day 90 and 110 (see Figure 10a), just after the release of parasitoids. As a result, more hosts can be found and parasitized by *E. formosa* during this early period, and a dramatic increase in numerical response of the parasitoid (more offspring) is the result. This prevents a high whitefly peak population later on.

Table 7. Effect of change of parameter-values in the model on the whitefly population in Experiment III. Effect is given as percentage reduction of the whitefly population (expressed as cumulative number of unparasitized prepupae + pupae during 100 days) and in number of adults per plant after 100 days.

Change in model	% Reduction of whitefly population during 100 days	Number of adults/ plant after 100 days
Experiment III	0.0	73
Parasitoids walking activity and walking speed as on tomato	9.4	66
Number of leaves = 20 at start of experiment	25.6	52
Whitefly life-history parameters of cv. 'Macho'	49.8	30
Temperature increase of 2 °C	(1)54.8	(1)16

(1) After 94 days instead of 100 days

Therefore, we conclude that it is especially glasshouse temperature causing success or failure of biological control of greenhouse whitefly on *Gerbera* in Experiment III. It was found earlier that with increasing temperature, the intrinsic rate of population increase r_m of the parasitoid *E. formosa* increases more than that of the greenhouse whitefly (van Roermund et al., 1997a). Thus, in terms of population growth, *E. formosa* is better off with a temperature increase than *T. vaporariorum*. In the present study, the simulated number of parasitoids in the crop was eventually 16 times higher after increasing the temperature by two degrees. Furthermore, a higher temperature leads to much better *E. formosa* dispersal and oviposition; below 18 °C parasitoids hardly fly and oviposit (van Roermund & van Lenteren, 1995). Average temperatures in commercially grown tomato crops in December and January are approximately 19 - 20 °C (new crop), in the early spring approximately 19 °C, and from May onwards 20 °C, with higher peaks between 13.00 - 16.00 h (personal communication, R.C.Kaarsemaker, Research Station for Glasshouse Vegetables and Ornamentals, Naaldwijk, The Netherlands). This is 2 degrees higher than in the commercial production of *G. jamesonii*. The difficulties of biological control of the greenhouse whitefly on *Gerbera* compared with tomato might thus be mainly a result of the relatively low average glasshouse temperature of the *Gerbera* crop in the winter and early spring period.

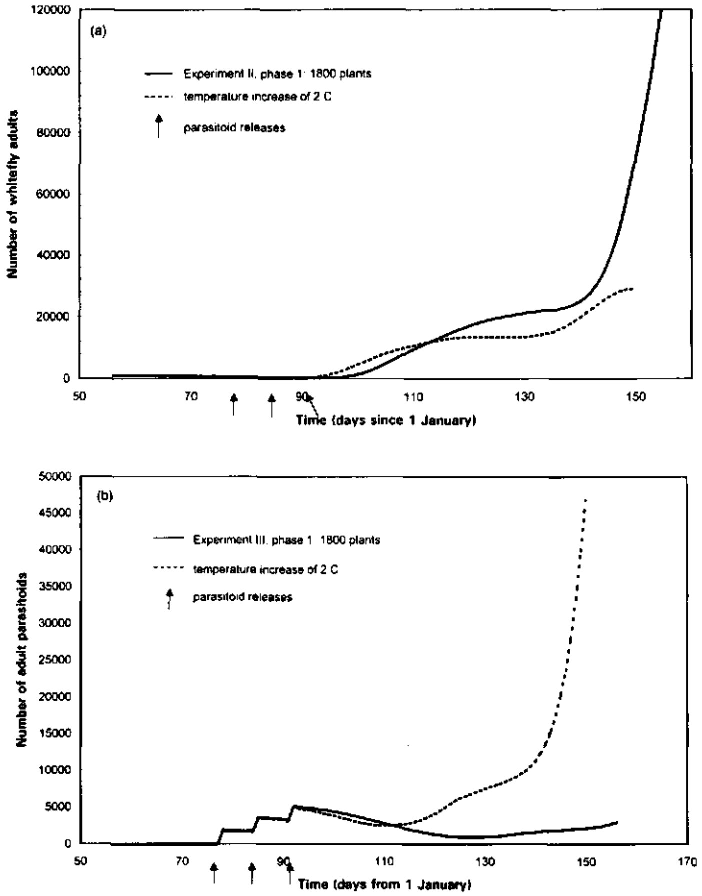

Figure 10. Simulated number of (a) whitefly adults and (b) adult *E. formosa* during the first phase of Experiment III and after a temperature increase of two °C. Arrows indicate the release of on average one parasitoid per plant.

A peak density of 16 whitefly adults per *Gerbera* plant as simulated by the model (Figure 10a) after temperature increase can be still too high and would not be accepted by most growers. So the number of released parasitoids (one parasitoid per plant, three times at weekly intervals) in Experiment III is still too small. This release strategy was based on the advice of Koppert Biological Systems for *Gerbera* crops at that time. Today, Koppert advices to release higher numbers (see below).

Final remarks

To sum up, plant architecture and searching behaviour of the parasitoid in the *Gerbera* crop form no obstacles for biological control. Also the leaf hairiness of *Gerbera* has hardly any negative influence on the degree of whitefly control. The total leaf area of *Gerbera* is larger than that of tomato, but also this larger leaf area does not explain failure of biological control. While evaluating different release strategies with the simulation model, it seemed best to release a high number of parasitoids (4 - 5 per plant) five times at weekly intervals. Koppert Biological Systems currently advises release of 1.5 *E. formosa* plus 1.5 *Eretmocerus californicus* per plant per week for at least five weeks, when a whitefly infestation is observed in a *Gerbera* crop and additional release(s) of parasitoids in the so-called hot-spots. Cultivar differences, as well as temperature have an important impact on biological control. Average glasshouse temperatures in commercial *Gerbera* crops are lower than in tomato crops early in the season. This lower temperature, together with a susceptible *Gerbera* cultivar can negatively influence whitefly biological control. So, our final conclusion is that measures such as (1) a higher average temperature (+2 °C) during winter and early spring, (2) informed choice of *Gerbera* cultivar use, and (3) higher release rates can result in reliable commercial biological control of greenhouse whitefly with *E. formosa* on *G. jamesonii.*

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CHAPTER 9

SUMMARISING DISCUSSION

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The interaction between the polyphagous, phytophagous greenhouse whitefly, *Trialeurodes vaporariorum*, its host plants and its parasitoid *Encarsia formosa* has been studied extensively on vegetables (e.g. Van Lenteren & Noldus, 1990, Noldus & van Lenteren, 1990, Van Lenteren et al., 1996, van Roermund et al., 1997a). This resulted into reliable biological control in major vegetable crops under commercial conditions (Van Lenteren, 2000; Van Lenteren & Woets, 1988). However, *T. vaporariorum* is also a prominent pest of ornamental crops. Because of pesticide resistance and governmental restrictions concerning extensive pesticide use, a search for control methods in ornamentals that are not based on conventional chemical control has started. This trend is reported both for the Netherlands as well as worldwide (Van Lenteren, 1990; Fransen, 1992; Albert et al., 1993; Benuzzi & Nicoli, 1993; Ravensberg & Altena, 1993; Gullino & Wardlow, 1999).

In order to develop biological control methods for ornamentals we chose to study the possibility for biological control of whiteflies on *Gerbera jamesonii*. To develop reliable biological control of the greenhouse whitefly on this crop, it is essential to know the tritrophic relationships between the host plant, the herbivorous insect and its parasitoids (Price et al., 1980). Based on a comparison of the biological data available for vegetables (tomato) and ornamentals (*Gerbera*) we expected that the following aspects could result in differences in biological control on tomato and *Gerbera*: (a) plant architecture (possible influence on the distribution of whiteflies on *Gerbera*, which may, for instance, result in lower encounter rates between parasitoid and host, and thus in less effective control of the pest), and (b) plant characteristics (plant characteristics such as trichomes were found to influence searching efficiency of *E. formosa* on cucumber cultivars: with increasing hair density fewer hosts were found (van Lenteren et al., 1995)). Many cultivars of *G. jamesonii* are known which differ in colour and shape of flowers and size, shape, texture and hairiness of leaves.

The hypotheses underlying research described in this thesis are therefore that (1) the rosette type host-plant shape of *G. jamesonii* leads to a whitefly dispersal and distribution that is different from that on vegetables such as tomato and cucumber, (2) plant characteristics such as leaf hairiness of *G. jamesonii* can negatively influence the searching behaviour of the parasitoid *E. formosa*, and (3) these characteristics taken together may lead to a failure of biological control of whitefly on *G. jamesonii*.

1. Does the different host-plant shape of *G. jamesonii* lead to a whitefly dispersal and distribution that is different from that on vegetables?

1.1 Movement and distribution of T.vaporariorum on G. jamesonii (chapter 2)

On the ornamental plant *G. jamesonii* the dispersal process of whiteflies is directed to the centre of the plant. This leads to adult and egg aggregation on young leaves on hairy as well as on non-hairy cultivars. About 80 % of emerged adults move from leaf of emergence to young leaves within a day. The almost complete horizontal movement of the whiteflies on *Gerbera* is quite different from observations on vegetable crops (El Khidir, 1963; Ohnesorge et al., 1980; Noldus et al., 1985; Xu Rumei, 1991). However, the ultimate result is similar: most adults alight and stay on the younger leaves. In a 'horizontal-level choice experiment' with *Gerbera* leaves, we found that first landings occur at random on the three leaf ages young, medium and old. Within 24 hours old and medium leaves are abandoned by the adult whiteflies. Although all three leaf types are used by adult whitefly females as feeding and oviposition sites, more than 50 % of adult whiteflies choose young leaves as feeding site within one hour. After 24 hours more than 70 % of adults is found on the young leaves. When different leaf ages are offered at the same horizontal level next to each other, approximately 70 % of the eggs are laid on young leaves. We can thus conclude that adult *T. vaporariorum* females prefer the young *Gerbera* leaves for feeding and oviposition. This preference for oviposition has also been shown for three citrus whitefly species on lemon (Walker & Zareh, 1990) and for *T. vaporariorum* on tomato (Noldus et al., 1985).

More immature whiteflies die during development on medium and old leaves compared to young leaves, but duration of development is the same on leaves of different ages. Mortality of whiteflies is much lower and fecundity is higher on young *Gerbera* leaves, which ultimately explains the selection of such leaves. The performance, in terms of survival and reproduction of whiteflies on different leaf types of a *Gerbera* plant, is thus linked to the preference of females for young leaves.

1.2 Whitefly dispersal and aggregation on G. jamesonii (chapter 3)

To determine the spatial distribution of whiteflies over *G. jamesonii*, we used an experimental crop situation with a fixed number of *Gerbera* plants and released a fixed number of *T. vaporariorum* females. After five days the whiteflies reached an average distance of 145 cm from the release point. The average dispersal speed by a whitefly female was 20 cm/h during the first five hours and dropped to 2-3 cm/h during the second and subsequent days, when females started to settle on leaves. In most cases a negative binomial distribution could be fitted to the observed spatial distribution of the whiteflies. Whitefly populations were strongly aggregated. Aggregation was density dependent, as is found in many herbivores: it increased with increasing whitefly density per plant. An aggregated distribution seems to be typical for the species, it is also found on tomato and cucumber plants (Ekbom, 1980; Noldus et al., 1986; Xu Rumei, 1991). Comparable average travel distances per day and same dispersal speeds are reported for whitefly on tomato (Noldus et al., 1986; van Vianen et al., 1988). Because travel distance and dispersal speed are similar for these very different crops, the influence of host-plant architecture on the dispersal and final distribution of *T. vaporariorum* in a crop seems to be minor.

An extremely aggregated distribution could lead to interference of herbivore individuals and, therefore, to a decrease in whitefly fitness. For example, on glasshouse vegetables Xu Rumei (1983) found a decrease in oviposition frequency at whitefly densities above 4 adults per cm^2. However, Yano (1988) reports no significant decrease in oviposition frequency at densities until 10 adults per cm^2. These extreme whitefly densities are rarely found in glasshouse crops in northern Europe.

The first hypothesis, i.e. that plant architecture of G. jamesonii *leads to a different whitefly dispersal and distribution on this plant compared to vegetable plants such as tomato, cucumber or sweet pepper, is rejected. Leaf selection behaviour and the resulting distribution of greenhouse whitefly observed on* Gerbera *was similar to that on vegetables.*

2. Do plant characteristics such as shape and leaf hairiness of *G. jamesonii* negatively influence the searching behaviour of the parasitoid *E. formosa* ?

2.1 Leaf surface of Gerbera plants and the parasitoid's searching behaviour (chapter 4)

To characterise the relation between the leaf surface of ten *G. jamesonii* cultivars and the parasitoid's *E. formosa* searching behaviour, the trichome density and shape are described. Both parameters vary largely among cultivars. The density varied from 80 to more than 1000 trichomes per cm^2 and the hair shape varied from single erect trichomes to tapestries of entangled trichomes above the leaf surface. To describe the parasitoid's searching behaviour, we used walking activity (percentage walking from the total time spent on a leaf), speed (distance moved per unit of time) and pattern (straightness of walking path). In spite of the differences in leaf surface structure the walking activity was around 75 % on most *Gerbera* cultivars. On tomato the wasp's walking activity is 70%. Walking speed greatly influences rates of parasitism by *E. formosa* on tomato plants on leaf and crop level (van Roermund et al., 1997 (a) and (b)). The walking speed on *Gerbera* is between 0.2 and 0.3 mm/s at 20 °C on all cultivars and was not significantly different from the speed on tomato. Hairs do hamper the parasitoids, because the walking speed on hairless sweet pepper is much higher (0.7 mm/s). For two cucumber cultivars with different hair densities, one cultivar having half the trichomes per cm^2 of the other, Li et al. (1987) reported a 0.1 mm/s difference in the walking speed of *E. formosa*. No negative linear relationship between walking speed and hair density is found on *Gerbera*, which is in contrast with data for cucumber where such a negative linear relationship has been reported (van Lenteren et al., 1995). That trichomes can slow down parasitoids and predators is also shown for *Trichogramma exiguum* on different plant species (Keller, 1987) and for *Phytoseiulus persimilis* on *Gerbera* cultivars (Krips et al., 1999). The walking speed of *T. exiguum* is much lower on woolly mullein (2.6 cm/min) compared to maize (12.4 cm/min) (Keller, 1987) and *P. persimilis* walks approximately two times faster on a *Gerbera* cultivar with 105 hairs cm^{-2} compared to two other cultivars with a leaf hair density of 400 and 730 hairs cm^{-2}, respectively (Krips et al., 1999). This results in a lower predation rate at higher trichome densities of *Gerbera* cultivars.

Wasps walk in a relatively straight line on all *Gerbera* cultivars. Li et al. (1987) reported that different leaf surfaces do not alter the shape of the walking track of *E. formosa* on two cucumber cultivars. However, the turning rate of the parasitoid *T. exiguum* is influenced by the leaf surface of different plant species (Keller, 1987). On maize, with erect trichomes arranged in rows, the walking paths have long straight sections, while on woolly mullein with forked trichomes and a dense pubescence, the turning rates are greater (Keller, 1987). On some *G. jamesonii* cultivars *E. formosa* females walked possibly on top of the dense pubescent layer of entangled trichomes and were not hampered in choosing a direction of the path. An increase in hair density leads to a decrease in encounter rate of *E. formosa* with whiteflies on cucumber (van Lenteren et al., 1995). Parasitism, host feeding, and the total number of whitefly hosts killed by four different *Encarsia* species were compared on two poinsettia cultivars differing in hairiness (Heinz & Parrella, 1994). The above mentioned three parameters are greater on the poinsettia cultivar with a 15 % lower trichome density for all four *Encarsia* species. An inverse relation between cotton trichome density and parasitism is also reported for *Heliothis* eggs parasitised by *Trichogramma* wasps (Schuster and Calderon, 1986). Bigler et al. (1988) report that travel speeds of *Trichogramma maidis* strains are positively related to performance of the parasitoids in the field: high travel speed means more parasitism.

So, although trichome density of plants is reported to influence the walking behaviour and searching efficiency of several predators and parasitoids, this seemed to play a limited role for *E. formosa* on *Gerbera*.

2.2 Gerbera plant architecture and pre- and post-landing response of E. formosa (chapter 5)

G. jamesonii leaves of all age classes were found and searched to the same extent by the parasitoid *E. formosa*, so architecture of this ornamental plant forms apparently no obstruction for *E. formosa* to locate its hosts. The preference of whitefly adults to oviposit on the young leaves (Noldus et al., 1985; Sütterlin et al., 1991; Walker and Zareh, 1990), results in high larval (L3, L4) densities on medium aged, full grown leaves. A preference of the parasitoid for these leaves would reduce the time needed to find a suitable host because of the accumulation of suitable hosts on these leaves, but such a preference was not found. On host-infested plants of the hairy cv. 'Parade', we found more parasitoids on medium aged leaves compared to leaves of other ages. However, this did not lead to more parasitizations of hosts on the hairy cultivar as will be discussed in one of the following sections.

In our experiments the number of landings on infested and uninfested *G. jamesonii* leaves was the same, suggesting that *E. formosa* females cannot distinguish infested and uninfested leaves from a distance. This confirms earlier data obtained in wind tunnel and olfactometer experiments with tomato plants by Noldus and van Lenteren (1990) as well as the recent olfactometer studies of Romeis and Zebitz (1997). The latter authors showed that a plant-host complex including visual clues such as a whole plant was attractive, while offering only odours of the plant-host complex was not. These results contradict the conclusion of Guerrieri (1997) that *E. formosa* is able to locate hosts from a distance. Guerrieri (1997) offered odours only, and worked with parasitoid females in a 'no-choice situation', whereas our studies included data on no-choice and choice experiments, with visual clues.

A redistribution of *E. formosa* takes place over time with increasing numbers of wasps on infested leaves, which explains the apparent misinterpretation by Hussey et al. (1976), Ledieu (1976) and Madueke (1979), that *E. formosa* is able to select infested leaves from a distance. These authors did not observe landings of individual wasps but based their conclusion on counts of wasps on leaves at a later time.

The dispersal process and redistribution of females on individual cut leaves was comparable to the situation on leaves of intact plants. Since distribution of *E. formosa* on the cultivars 'Fame' (112 trichomes cm^{-2}) and 'Parade' (338 trichomes cm^{-2}) was the same we may conclude that the difference in hair density between these cultivars apparently has no influence on parasitoid distribution. In addition, also the whitefly distribution on these cultivars was the same (**chapters 2 and 3**). However, in the intact plant situation we found a higher percentage parasitoids on the leaves and more parasitizations per parasitoid on the less hairy cv. 'Fame', compared to the hairy cv. 'Parade' when host density was high.

Parasitoids were observed more often on the abaxial than on the adaxial of infested and uninfested leaves. However, on tomato females showed no preference for the adaxial or abaxial leaf side on uninfested leaves, but were arrested on the abaxial leaf side after encountering hosts (van Roermund and van Lenteren, 1995; van Roermund et al., 1994;). Arrestment after encountering hosts at the leaf underside was also observed on *Gerbera* leaves (**chapter 6**). In a simulation study on tomato van Roermund et al. (1997a) showed that staying longer on the lower leaf side, where hosts are normally found, results in a higher number of host encounters and ovipositions.

2.3 Foraging behaviour of the parasitoid on Gerbera (chapter 6)

Insight into the foraging behaviour of the parasitoid *E. formosa* was gained by observing individual parasitoids on leaves of *G. jamesonii*, until females left the leaf. In comparison to tomato only minor differences in foraging behaviour occurred except for the residence time of females which was approximately three to four times longer on the seven times larger *G. jamesonii* leaves.

On uninfested *Gerbera* leaves females searched for approximately 1.5 h before they left. Encounters with hosts clearly arrested the parasitoid on the leaf, because the mean residence time on infested leaves was approximately 3.5 h. Residence times did not differ significantly between plant cultivars with different leaf structure and hairiness. On tomato leaves the parasitoids were also arrested by host encounters (van Roermund et al., 1994). This is predicted for patchily distributed hosts such as whiteflies (Waage, 1979) because host encounter rates and egg laying of parasitoids increases when host density is locally high. This arrestment effect was found for many other parasitoids such as aphid parasitoids (van Steenis et al., 1995) and *Drosophila* parasitoids (van Alphen & Galis, 1983; van Lenteren & Bakker, 1978). With patches of one or a few hosts and uniformly distributed hosts Driessen et al. (1995) showed that oviposition by *Venturia canescens* did not lead to arrestment but to earlier departure from the leaf. For *E. formosa* the variation in residence time was high on tomato and *Gerbera* which makes quantification of time allocation difficult. Therefore, van Roermund et al. (1994) analysed their foraging data with a proportional hazards model, and leaving of the patch by the parasitoid appeared to be characterized by a constant probability per unit of time. This has been incorporated in the model of *E. formosa's* foraging behaviour in a *Gerbera* crop. This submodel is used in the simulation model described in **chapter 8**. The high variability of GUTs found in our experiment is not uncommon for parasitoids. It is also mentioned for *E. formosa* on tomato leaves (van Roermund et al., 1994), for *Aphidius colemani* on cucumber leaves (van Steenis et al., 1995) and for *V. canescens* on wheat (Waage, 1979).

When hosts were offered at an equidistant position from the parasitoid, host encounter rate was the same on tomato and *G. jamesonii* despite their difference in leaf structure. This result was expected because only very small differences in walking activity and walking speed were found between these plant species (**chapter 4**). However, in a "natural host distribution - intact plant situation", differences in number of encounters between parasitoids and hosts on different *G. jamesonii* cultivars led to differences in number of ovipositions, and the total killing rate of hosts was larger on the hairy cultivar 'Tennessee' (363 trichomes per cm^2).

Walking activity and host encounter rates that resulted in an oviposition, decreased with decreasing egg load of the parasitoid. This decreasing walking activity with egg depletion was also found for *E. formosa* when searching and ovipositing on cucumber (van Roermund and van Lenteren, 1995). A decreasing relation of both walking activity and host acceptance with the number of eggs laid by *E. formosa* may be based on the same relationship with the physiological parameter egg load. Such a relation was also found for a number of other parasitoids as reviewed by Minkenberg et al. (1992). We found an interesting extra phenomenon: the parasitoids' walking activity and host acceptance did increase again after eight ovipositions. We hypothesize that this is caused by maturation of eggs in the ovarioles after the first ovipositions, a process that takes a certain amount of time and results in an increased egg load with time.

In summary, a large number of behavioural elements of the parasitoid is very similar or the same among different *Gerbera* cultivars and/or different whitefly host plants, and a number of foraging elements is different among *Gerbera* cultivars and/or different host plants. These similarities and differences are summarized in Table 1.

The second hypothesis, i.e. that plant characteristics of G. jamesonii *could influence the searching behaviour of* E. formosa *for its whitefly host negatively, is not supported by our data. The searching efficiency of* E. formosa *on* Gerbera *is as good as on the vegetable tomato.*

Table 1. Effect of different host plants and/or different *G. jamesonii* cultivars on behavioural elements of *E. formosa*.

	Effect	
Behavioural element	Host plants	*Gerbera* cultivars
Landing on leaf sides	at random (tomato) vs. 75 % abaxial (*Gerbera*)	same: 75 % abaxial
Searching on different leaf ages	not investigated	same
Parasitoid distribution	not investigated	same
Walking activity	same (tomato/*Gerbera*)	same
Walking speed	same (tomato/*Gerbera*)	same
Encounter rate with first host	same (tomato/*Gerbera*)	not investigated
Antennal + ovipositorial rejection	same (tomato/*Gerbera*)	same
Number of host encounters + ovipositions	not investigated	larger on cv. Tennessee
Decreasing walking activity with egg load	same (cucumber/*Gerbera*)	same
After 8 ovipositions increase of walking activity + host acceptance	not investigated	same
Giving up times underestimated	not investigated	same
Residence times	shorter on tomato vs. *Gerbera*	same
Total killing rate	not investigated	larger on cv. Tennessee
Parasitizations per parasitoid	not investigated	more on cv. Fame (high density)

3. Do host plant architecture and leaf characteristics of *G. jamesonii* lead to failure of whitefly biological control on *Gerbera*?

3.1 Biological control of whitefly on G. jamesonii: small glasshouses (chapter 7)

One central release of on average three parasitoids per plant at three weeks after whitefly introduction in small glasshouses (60 m^2) resulted in sufficient pest control.

The percentage parasitism of whitefly on *G. jamesonii* in these experiments was higher (range: 58 - 80 %) than and was achieved with less than half of the *Encarsia formosa* density per plant described for tomato by Eggenkamp-Rotteveel Mansveld et al. (1982 a and b), while the initial whitefly density was much lower in Eggenkamps experiments. Less than 5 % of the plants was infested there and the average number of white pupae per plant was 0.008. However, our experiments were done in a much smaller glasshouse which may have facilitated the finding of whiteflies by the parasitoids. The only data on commercial application of *E. formosa* to control whitefly in *Gerbera* are from Blümel (1992). In two commercial glasshouses each with about 500 plants, parasitism maximally reached 90 % during a 36 week period (Blümel, 1992), although mean percentages of parasitism were much lower. Blümel released a total of about 50 parasitoids per plant and biological control was considered to be successful by the author.

3.2 Biological control of whitefly on G. jamesonii: a larger glasshouse (chapter 8)

Biological control of greenhouse whitefly with the parasitoid *E. formosa* was successful on *Gerbera* in small glasshouses (**chapter 7**), but failed in a larger glasshouse (**chapter 8**). The introduction of on average two parasitoids per plant in three releases in a crop of 1800 *Gerbera* plants was not sufficient to control whitefly. A sharp increase in number of adults was seen 40 days after starting the experiment. This resulted in large numbers of whiteflies (38 adults) per plant after 85 days, and numbers still increased thereafter.

3.3 Putting the puzzle together: what makes biological control successful or not in Gerbera? (Chapter 8)

Possible explanations for the failure of biological control of *T. vaporariorum* on *Gerbera* are:

(1) A too high initial whitefly density: too many whiteflies may be present at the start of the experiment.

(2) A wrong release strategy: more parasitoids should be introduced and/or at a higher frequency.

(3) Hampered locomotion of the parasitoid: because of the *Gerbera* leaf hairiness, parasitoids walk too slow and, therefore, encounter too few hosts.

(4) A too large leaf area of the crop: the total leaf area of the canopy in the large glasshouse experiment was so high that the parasitoids found insufficient whiteflies.

(5) A cultivar effect: some *G. jamesonii* cultivars may stimulate whitefly development or hamper parasitoid activity, resulting in insufficient control.

(6) A too low glasshouse temperature: the searching efficiency of parasitoids is too low.

(1)Initial whitefly population. The initial whitefly numbers released in the large glasshouse were 0.5 to 0.6 adults per plant, while the initial density in the small glasshouse was two adults per plant. In another glasshouse (**chapter 7**) in which biological control was successful two *T. vaporariorum* adults per plant were initially released. So, the initial whitefly population was not too high for successful control.

(2) Release strategy. Five parasitoid releases of 4 – 5 parasitoids per plant, with a weekly interval, beginning the third week after whitefly introduction is the best strategy according to the simulation model. Obviously, this is the strategy with most parasitoids released per plant. However, even this strategy does not lead to very low numbers of greenhouse whitefly in the large glasshouse. Koppert Biological Systems advices 1.5 E. formosa per plant plus 1.5 Eretmocerus per plant. Additional releases of parasitoids in so-called hot-spots are recommended. This seems, based on practical experience, to be sufficient.

(3) Parasitoid walking behaviour. The hypothesis that leaf hairiness of *Gerbera* negatively influences the foraging behaviour of the parasitoid as was found for cucumber (van Lenteren et al., 1995), for four different *Encarsia* species on Poinsettia cultivars (Heinz & Parella, 1994) and for the predator *Phytoseiulus*

persimilis on *Gerbera* (Krips et al., 1999), was rejected after experimental studies on a laboratory scale (**chapters 4** and **5**), and also after studying this with a simulation model on glasshouse scale for *Gerbera* (**chapter 8**). Changing the input parameters walking activity and walking speed of the parasitoid on *Gerbera* leaves to those obtained on tomato only resulted in a slight decrease (<10 %) of the whitefly population.

(4) Total leaf area. In the model it is assumed that *E. formosa* searches all leaves, host-infested or not, in the canopy. More leaves and thus total leaf area in a canopy decreases the encounter probability of the parasitoid with its host. Reducing the initial number of leaves per *Gerbera* plant in the model from 40 to 20, eventually only showed a 25 % reduction of the whitefly population.

(5) Gerbera cultivar differences. Development rate of whiteflies and, to a lesser extent, fecundity are important parameters for the whitefly population development, according to the sensitivity analysis of the model for tomato (Van Roermund & van Lenteren, 1997). The importance of the development rate of a herbivore for the population growth on different *Gerbera* cultivars (Krips et al., 1998) and its impact on biological control of the herbivore was also stressed by Krips et al. (1999). When the input parameters for development duration and fecundity of *T. vaporariorum* for *Gerbera* cv. 'Macho' (a relatively "poor" cultivar) were used in the model, a 50 % reduction of the whitefly population under biological control was achieved. We showed that differences between life history parameters of *T. vaporariorum* on different *Gerbera* cultivars exist, while it was argued before that development of the greenhouse whitefly was not influenced by different *G. jamesonii* cultivars (Dorsman & van de Vrie, 1987 and unpublished). However, according to the model, these differences in *Gerbera* cultivars could not fully explain the failure of biological control in the large glasshouse.

(6) Glasshouse temperature. Temperatures in tomato crops are on average 2 °C degrees higher than in *G. jamesonii* crops in winter and spring. Temperature appears important for success or failure of biological control of greenhouse whitefly on *Gerbera*. When we increased the temperature by 2 °C in the *Gerbera* glasshouse, the simulated whitefly population was larger at the start of the experiment. This higher host density enabled *E. formosa* to encounter and parasitize more whitefly immatures, resulting in a strong numerical response of the parasitoid. It was found earlier that with increasing temperature the intrinsic rate of population increase of the parasitoid *E. formosa* increases faster than that of the greenhouse whitefly (van Roermund et al., 1997a). Thus, in terms of population growth, *E. formosa* does better at a higher temperature than *T. vaporariorum*. In the crop where the temperature was 2°C higher, the simulated number of parasitoids was eventually 16 times higher. Also a higher temperature leads to better *E. formosa* dispersal and oviposition, because parasitoids are inactive below 18 °C (Van Roermund & van Lenteren, 1995).

The third hypothesis, i.e. that host-plant architecture and leaf hairiness of Gerbera *negatively influences the searching behaviour of* Encarsia formosa *is not supported by our results. This conclusion is based on our experimental data* *and computer simulations. Surprisingly, and as a result of integrating all parameters for crop, pest, natural enemy and glasshouse temperature, we found that it is mainly the glasshouse temperature that determines success or failure of biological control in* Gerbera.

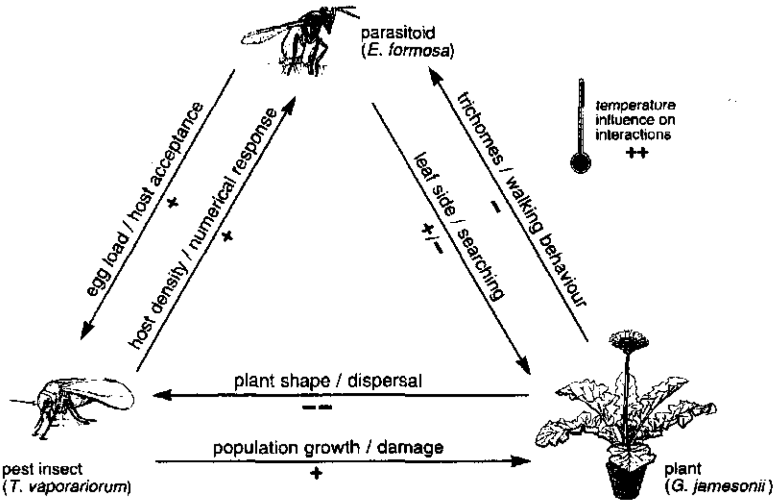

Figure 1. Interactions between *Gerbera*, whitefly and the parasitoid *Encarsia formosa*. Positive and negative effects are indicated; interactions have been studied as part of this thesis.

With an adjustment of the release strategy, the right choice of the most resistant *Gerbera* cultivars, and a slight increase of glasshouse temperature, biological control of *T. vaporariorum* on *G. jamesonii* will be successful. Currently, Koppert advises at least five (preventive) releases of 1.5 *E. formosa* plus 1.5 *Eretmocerus californicus* per plant at weekly intervals (Koppert Biological Systems, unpublished) at very low whitefly densities. Very few growers used *E. formosa* to control whitefly in *Gerbera* when we started this project in 1990. Nowadays, more than 90 % of the Dutch *Gerbera* area is under biological whitefly control (van Mei, pers. com.), a quite positive development!

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ABSTRACT

In this thesis fundamental and applied research is described that was initiated to develop biological control of whitefly with the parasitoid *Encarsia formosa* in the ornamental *Gerbera jamesonii* Hook (Campanulales: Compositae).

To test the hypothesis that host plant architecture of *G. jamesonii* results in a different whitefly distribution pattern when compared with vegetables such as tomato and cucumber, we started studying whitefly dispersal behaviour and the choice of oviposition and feeding sites of the greenhouse whitefly within a plant. The behaviour of the herbivore was compared on two cultivars of *G. jamesonii*, differing in hairiness. The dispersal process of whiteflies was directed to the centre of the plant. This leads to adult and egg aggregation on young leaves on the hairy as well as on the less-hairy cultivar. Three parameters (development time, mortality and fecundity) to measure performance of *T. vaporariorum* were investigated, to determine a possible link with preference for certain leaves or cultivars by whitefly adults. Development duration of immatures is the same on leaves of different ages. Mortality of whiteflies is much lower and fecundity is higher on young *Gerbera* leaves. The dispersal and aggregation of whitefly adults between plants was investigated next. Whitefly populations were strongly aggregated on *Gerbera*, which seems typical for this whitefly species. Travel distance and dispersal speed were similar on very different crops such as *Gerbera* and tomato. Leaf selection behaviour and the resulting distribution of greenhouse whitefly on *Gerbera* was similar to that on vegetables. The first hypothesis that differences in host plant architecture result in different whitefly distributions is, thus, rejected.

The second hypothesis that plant characteristics such as shape and leaf hairiness of *G. jamesonii* negatively influence the searching behaviour of the parasitoid *E. formosa* was tested next. Trichome density of *Gerbera* cultivars appeared to influence the walking behaviour (walking speed, walking activity and straightness of walkng path) and searching efficiency of *E. formosa* only slightly. *Gerbera* leaves of all age classes were found and searched by the parasitoid. Number of landings was the same on infested and uninfested *Gerbera* leaves; parasitoids were observed more often on the abaxial side of the leaves, where hosts are found normally. The foraging behaviour of *E. formosa* on leaves of a range of *Gerbera* cultivars is comparable. The searching efficiency of *E. formosa* on *Gerbera* is as good as on the vegetable tomato, so also the second hypothesis that plant characteristics negatively influence the searching behaviour of *Encarsia* on *Gerbera*, is rejected.

The third hypothesis that plant architecture and leaf characteristics of *G. jamesonii* lead to failure of whitefly biological control on *Gerbera* was tested in glasshouses. Glasshouse studies are essential to validate the conclusions based on small population experiments and laboratory experiments. One central release of on average three parasitoids per plant, three weeks after whitefly introduction resulted in successful pest control in a small glasshouse of 60 m^2. Sufficient control was not achieved in a larger glasshouse (300 m^2).

Possible explanations for the failure of biological control in *Gerbera* were evaluated with a simulation model of *G. jamesonii*, *T. vaporariorum* and *E. formosa*. Surprisingly, and as a result of integrating all parameters for crop, pest, natural enemy and glasshouse temperature, we found that it is mainly the glasshouse temperature that determines success or failure of biological control in *Gerbera*.

With an adjustment of the release strategy of parasitoids, the right choice of (partially) resistant *Gerbera* cultivars, and a slight increase of glasshouse temperature in early spring, biological control of *T. vaporariorum* on *G. jamesonii* will be successful.

SAMENVATTING

Het hier beschreven onderzoek heeft de ontwikkeling van biologische bestrijding van kaswittevlieg (*Trialeurodes vaporariorum*) met behulp van de sluipwesp *Encarsia formosa* in het sierteeltgewas *Gerbera jamesonii* Hook (Campanulales: Compositae) tot doel.

In dit proefschrift wordt als eerste de hypothese getoetst dat de specifieke waardplant-architectuur van *Gerbera* een afwijkend wittevlieg-verdelingspatroon tot gevolg zou hebben. De verdeling wordt vergeleken met die van groentegewassen, zoals tomaat en komkommer. De hypothese is getoetst aan de hand van het verspreidingsgedrag van kaswittevliegen binnen een plant en de plaats die voor eileg en voeding werd gekozen. Het gedrag van de herbivoor is vergeleken op twee in bladbeharing verschillende *Gerbera* cultivars. De verspreiding was horizontaal gericht naar het hart van de plant en leidde tot aggregatie van adulten en eieren op de jonge bladeren, van zowel de sterk behaarde als de minder behaarde cultivar. Drie parameters (ontwikkelingsduur, mortaliteit en fecunditeit) die een maat zijn voor de zogenaamde performance van *T. vaporariorum* zijn onderzocht om een mogelijk verband tussen de parameter en de voorkeur voor bepaalde bladeren of cultivars te ontdekken. De ontwikkelingsduur van wittevlieg is dezelfde op in leeftijd verschillende bladeren. De mortaliteit is veel lager en de fecunditeit is hoger op jonge *Gerbera* bladeren. Daarna zijn verspreiding en aggregatie van wittevlieg-adulten tussen planten bestudeerd. Wittevliegpopulaties zijn op *Gerbera* sterk geaggregeerd, hetgeen kenmerkend voor deze wittevliegsoort schijnt te zijn. De afgelegde afstand en de verspreidingssnelheid van wittevliegen waren op zeer uiteenlopende gewassen, zoals *Gerbera* en tomaat hetzelfde. De bladkeuze van wittevliegen en de daaruit volgende verdeling op *Gerbera* was vergelijkbaar met die op groentegewassen. De eerste hypothese, dat een verschillende waardplantarchitectuur tot een verschillende wittevliegverdeling leidt is daarom verworpen.

De tweede hypothese luidt dat kenmerken van planten, zoals vorm en bladbeharing van *G. jamesonii* het zoekgedrag van de parasitoid *Encarsia formosa* negatief beïnvloeden. Bladhaardichtheid van *Gerbera*cultivars beïnvloedt het loopgedrag (loopsnelheid, loopactiviteit en rechtlijnigheid van het zoekpad) en de zoekefficiëntie van *E. formosa* slechts in geringe mate. *Gerbera*bladeren van alle leeftijdsklassen zijn door de sluipwesp gevonden en afgezocht. Het aantal landingen was op met wittevlieg geïnfecteerde en niet-geïnfecteerde *Gerbera*bladeren hetzelfde. Parasitoiden zijn vaker op de onderkant dan op de bovenkant van bladeren geobserveerd, waar gastheren gewoonlijk ook te vinden zijn. Het fourageergedrag van *E. formosa* op het blad van een reeks verschillende *Gerbera*cultivars is vergelijkbaar. De zoekefficiëncie van *E. formosa* op *Gerbera* is vergelijkbaar met die op het groentegewas tomaat. De tweede hypothese wordt daarmee eveneens verworpen.

De derde hypothese, dat plantenarchitectuur en bladkenmerken van *Gerbera* tot mislukking van de biologische bestrijding van kaswittevlieg op *Gerbera* zouden leiden werd in kassen getoetst. Kasstudies zijn essentieel om conclusies te staven, die op kleine populatieproeven en laboratoriumproeven

gebaseerd zijn. Een eenmalig centraal loslaten van gemiddeld drie parasitoiden per plant, drie weken na het introduceren van de wittevlieg had een succesvolle plaagbestrijding tot gevolg in een kleine kas van 60 m^2. In een grotere kas (300 m^2) konden we onvoldoende bestrijding realiseren.

Mogelijke verklaringen voor het mislukken van biologische bestrijding van wittevlieg in *Gerbera* zijn met behulp van een simulatiemodel van *G. jamesonii, T. vaporariorum* en *E. formosa* onderzocht. Verrassend, en door integratie van alle parameters voor gewas, plaaginsect, natuurlijke vijand en kastemperatuur, werd duidelijk dat het hoofdzakelijk de kastemperatuur is die succes of mislukking van biologische bestrijding in *Gerbera* teweegbrengt.

Met een aanpassing van de *Encarsia*-loslaatstrategie, de goede keuze van (partieel) resistente *Gerbera*cultivars en een geringe kastemperatuur-verhoging in het vroege voorjaar zal biologische bestrijding van *T. vaporariorum* op *G. jamesonii* succesvol zijn.

ZUSAMMENFASSUNG

In der vorliegenden Forschungsarbeit werden Untersuchungen beschrieben, die zur Entwicklung von biologischer Schädlingsbekämpfung der Weissen Fliege (*Trialeurodes vaporariorum*) mit dem Parasitoiden *Encarsia formosa* im Zierpflanzengewächs *Gerbera jamesonii* Hook (Campanulales: Compositae) führen sollten.

Es existieren viele verschiedene *G. jamesonii* Sorten, die sich unterscheiden durch Pflanzeneigenschaften, wie beispielsweise Farbe und Form der Blüten und Grösse, Form, Beschaffenheit und Behaarung der Blätter. Diese Eigenschaften können die Entwicklung von pflanzenfressenden Insekten positiv und auch negativ (das wird Wirtspflanzenresistenz genannt) beeinflussen und ebenfalls den Erfolg von natürlichen Feinden bei biologischer Schädlingsbekämpfung beeinflussen. Auf einige bereits untersuchte Faktoren konnten wir uns zu Anfang des Forschungsprojektes berufen: die Wachstumsrate einer Weissen Fliege-Population ist beispielsweise vergleichbar auf einer Anzahl Gerberarassen und auch vergleichbar mit der Rate des Gemüsegewächses Tomate. In Gewächshaustomaten ist biologische Schädlingsbekämpfung der Weissen Fliege mit dem Nützling *E. formosa* erfolgreich. Deshalb erwarten wir ausschliesslich einen Effekt von Pflanzeneigenschaften auf das eigentliche Verbreiten und die Verteilung des Schädlings im Gewächs. Bekannt ist auch, dass Pflanzeneigenschaften, wie beispielsweise Blatthaare, die Sucheffizienz der Schlupfwespe *E. formosa* in verschiedenen Gurkensorten beeinflussen: mit zunehmender Haardichte werden weniger Wirtstiere gefunden.

Die zu untersuchenden Hypothesen der Forschungsarbeit lauten: (1) die Rosettenstruktur der Zierpflanze *G. jamesonii* führt zu einer Verbreitung und Verteilung der Weissen Fliege, die sich deutlich unterscheidet von der auf Gemüsegewächsen, wie beispielsweise Tomate und Gurke, (2) Pflanzeneigenschaften, z.B. räumliche Struktur und Blattbehaarung von *G. jamesonii*, können das Suchverhalten von *E. formosa* nachteilig beeinflussen und (3) die genannten Eigenschaften zusammen besehen, können biologische Schädlingsbekämpfung der Weissen Fliege unmöglich machen.

Um die erste Hypothese zu untersuchen, werden die Verbreitung der Weissen Fliege und Wahl des Eiablage- und Nahrungsaufnahmeortes der Adulten auf einer Pflanze studiert. Das Verhalten des Pflanzenschädlings wird auf zwei unterschiedlich behaarten Gerberarassen verglichen. Die Verbreitung der Weissen Fliege ist auf die Pflanzenmitte hin orientiert. Das führt zu Häufung von Adulten und Insekteneiern auf den jungen Blättern, bei sowohl der behaarten, als auch der wenig behaarten Rasse. Drei Parameter (Entwicklungsdauer, Mortalität und Fruchtbarkeit) für die sogenannte 'performance' der Weissen Fliege werden bestimmt und gekoppelt an das Bevorzugen bestimmter Blattlagen der Adulten. Auf Blättern verschiedenen Alters ist die Entwicklungsdauer der Weissen Fliege dieselbe. Auf jungen *Gerbera* Blättern findet sich jedoch eine niedrigere Mortalität und höhere Fruchtbarkeit der Weissen Fliege. Verbreitung und Häufung von Adulten werden ebenfalls auf mehreren Gerberapflanzen untersucht. Ein starkes Aggregieren von Populationen auf *Gerbera* scheint

characteristisch für diese Weisse Fliege-Art zu sein. Zurückgelegte Distanz und Verbreitungsgeschwindigkeit stimmen auf sehr unterschiedlichen Gewächsen, wie *Gerbera* und Tomate, überein. Die Blattwahl und die daraus folgende Verteilung der Weissen Fliege ist auf *Gerbera* und Gemüsegewächsen gleich. Die Hypothese, dass Unterschiede in der Wirtspflanzenarchitektur zur unterschiedlichen Verteilung der Weissen Fliege auf den verschiedenen Pflanzen führen, wird deshalb zurückgewiesen.

Als nächstes wird die Untersuchung der zweiten Hypothese beschrieben, sie lautet: Pflanzeneigenschaften, wie beispielsweise Form und Blattbehaarung von *G. jamesonii* beeinflussen das Suchverhalten der Erzwespe *Encarsia formosa* nach ihrem Wirtstier negativ. Blatthaardichte von Gerberasorten beeinflussen das Laufverhalten (gemessen sind Geschwindigkeit, Aktivität und Geradlinigkeit des Laufpfades) und die Sucheffizienz von *E. formosa* nur sehr begrenzt. Gerberablätter allen Alters werden durch Parasitoiden gefunden und abgesucht. Die gleiche Anzahl Landungen wird auf nicht-infizierten und infizierten Gerberablättern observiert; Parasitoiden werden meist auf der Unterseite von Blättern gefunden, wo die Wirtstiere sich normalerweise befinden. Das Fouragierverhalten von *E. formosa* ist auf Blättern einer Reihe verschiedener Gerberasorten vergleichbar. Die Sucheffizienz der Schlupfwespe auf *Gerbera* und Tomate kommt überein, weshalb auch die zweite Hypothese zurückgewiesen wird.

Die dritte Arbeitshypothese wird in Gewächshäusern getestet, sie lautet: Pflanzenarchitektur und Blatteigenschaften von *G. jamesonii* führen zum Misslingen von biologischer Schädlingsbekämpfung der Weissen Fliege in *Gerbera*. Gewächshausstudien sind essentiell bei der Bewertung der Schlussfolgerungen aus Experimenten mit kleinen Populationen und von Laborexperimenten. Ein einmaliges, zentrales Einsetzen von durchschnittlich drei Parasitoide pro Pflanze, drei Wochen nach der Einführung der Weissen Fliege, führt zu erfolgreicher Schädlingsbekämpfung in einem kleinen, 60 m^2 Gewächshaus. Ausreichende Bekämpfung der Weissen Fliege wird jedoch in einem grösseren Gewächshaus (300 m^2) nicht erzielt. Mögliche Erklärungen für das Misslingen der biologischen Schädlingsbekämpfung werden mit Hilfe eines Simulationsmodells von *G. jamesonii, T. vaporariorum* und *E. formosa* bewertet. Überraschenderweise, und folgend aus der Integration aller Parameter für Gewächs, Schädling, Nützling und Gewächshaustemperatur, können wir feststellen, dass es hauptsächlich die Gewächshaustemperatur ist, die Erfolg oder Misslingen der biologischen Schädlingsbekämpfung in *Gerbera* bestimmt.

Mit einer Anpassung der Nützlingseinsatzstrategie, der richtigen Wahl (partiell) resistenter Gerberasorten und einer leichten Erhöhung der Gewächshaustemperatur im frühen Frühjahr wird biologische Schädlingsbekämpfung von *T. vaporariorum* mit der Schlupfwespe *E. formosa* in *G. jamesonii* zum Erfolg!

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Susanne

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CURRICULUM VITAE

In 1982 voltooide ik, Susanne Sütterlin (4 december 1962, Lörrach, Duitsland) mijn schoolopleiding aan het Hans-Thoma-Gymnasium te Lörrach (cum laude). Na driekwartjaar in Nederland te hebben gewoond, deed ik 1983 toelatingstentamen Nederlande Taal in Utrecht en begon mijn studie biologie aan de Vrije Universiteit te Amsterdam, alwaar in 1985 het Propedeutisch Examen biologie werd behaald. De doktorale studie volgde ik aan de Rheinische Friedrich-Wilhelms Universität te Bonn, Duitsland en met behulp van een stipendium (door de Deutsche Akademische Austauschdienst) zette ik de studie voort aan de Universiteit Utrecht, alwaar in 1989 het Doktoraal Examen biologie werd behaald. Leeronderzoeken werden verricht in de vakken Ethologie en Entomologie, met de onderwerpen (1) sociaal gedrag, in het bijzonder het samenwerken bij chimpansees in een intact groepsverband, Burgers Zoo te Arnhem en (2) oecologie en biologische bestrijding van mineervliegen in het sierteeltgewas *Gerbera*, gedeeltelijk uitgevoerd op het Proefstation voor Bloemisterij en Glasgroente, te Aalsmeer. In het najaar van 1989 werd aan Wageningen Universiteit bij het Laboratorium voor Entomologie begonnen met het promotieonderzoek (in deeltijd) beschreven in dit proefschrift. Sinds 1997 werk ik als onderzoeker binnen de afdeling Onderzoek & Ontwikkeling bij Naktuinbouw, waar ik verantwoordelijk ben voor de groep 'Insectenresistentie-toetsingen'.