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Amitus fuscipennis, an alternative to the biological control of *Trialeurodes vaporariorum* by *Encarsia formosa*?

Raf M. J. De Vis[1,3], Joop C. van Lenteren[2]
[1]*Centro de Investigaciones y Asesorías Agroindustriales, Universidad de Bogotá Jorge Tadeo Lozano, Cundinamarca, Colombia*
[2]*Laboratory of Entomology, Wageningen University, The Netherlands*
[3]*Current address: Research Station for Vegetable Production, Sint-Katelijne-Waver, Belgium*

Abstract

Biological control of *Trialeurodes vaporariorum* (Homoptera Aleyrodidae) by *Amitus fuscipennis* (Hymenoptera Platygastridae) with or without *Encarsia formosa* (Hymenoptera Aphelinidae) was tested in both a glasshouse and a plastic greenhouse during two consecutive production cycles of a beef tomato crop on the Bogotá Plateau in Colombia. The mean temperature was around 16 °C in the plastic greenhouse and around 17 °C in the glasshouse. *A. fuscipennis* was introduced at a rate of 5 pupae per m^2 per week during the first 13 weeks of the first cycle. During the second cycle, 2.5 pupae of both *E. formosa* and *A. fuscipennis* per m^2 per week were introduced during the first 13 weeks. During the first cycle, control was obtained for 5 months in the plastic greenhouse and 3 months in the glasshouse, after which the population of *T. vaporariorum* adults increased to a maximum of 50 adults per plant. Parasitism was initially higher than 80% but then decreased to 56% in the plastic greenhouse and to 20% in the glasshouse. During the second cycle, biological control was successful in both greenhouses. Populations of *T. vaporariorum* were lower than 1.2 adults per plant and parasitism, caused mainly by *E. formosa*, was near 90% most of the time. Therefore, *E. formosa* is recommended to keep populations of *T. vaporariorum* at low levels in unheated greenhouses on the Bogotá Plateau. When high populations of *T. vaporariorum* are to be expected or control of high-density spots is required, *A. fuscipennis* could be a beneficial addition to *E. formosa*.

Key words: Greenhouse experiment, biological control, *Trialeurodes vaporariorum*, Homoptera, Aleyrodidae, *Encarsia formosa*, Hymenoptera, Aphelinidae, *Amitus fuscipennis*, Platygastridae, high altitude tropics.

Introduction

The protected cultivation of tomatoes is a recent development in Colombia, and has generally replaced field-grown tomatoes. The high risk due to pests and diseases in field production, which can sometimes cause total loss of the crop, is one of the reasons that brought about the change to greenhouse production. The use of greenhouses reduces pest and disease risks, and increases production and profits. Greenhouses are currently used for tomato production in the intermediate climate zone (altitude 1800-2000 m) where field-grown tomatoes are traditionally cultivated, but are also used in cold climate zones such as the Bogotá Plateau (altitude 2665 m). One of the advantages of the production of greenhouse tomatoes on the Bogotá Plateau is the reduced pest spectrum. From 1995 on, greenhouse tomatoes have been produced at the Horticultural Research Centre of the University of Bogotá Jorge Tadeo Lozano, where the most important pest has been greenhouse whitefly *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae). Leafminers and aphids are generally kept at low densities by naturally occurring parasitoids (De Vis and van Lenteren, 1999).

Biological control of pests on greenhouse grown tomatoes has become a common practice around the world (van Lenteren and Woets, 1988). The parasitoid *Encarsia formosa* Gahan (Hymenoptera Aphelinidae) is traditionally used for biological control of the greenhouse whitefly (van Lenteren, 1992, 1995, 2000). The greenhouse temperature on the Bogotá Plateau is lower than the mean temperature in the climate-controlled greenhouses in Western Europe (in Colombia, mean temperatures are 15-16 °C, with day temperatures of 18-22 °C and night temperatures of 5-12 °C). In commercial greenhouses in the temperate zones, the mean temperature is around 20 °C. At that temperature, the intrinsic rate of increase (r_m) of *E. formosa* is considerably higher than that of *T. vaporariorum*. In contrast, at 15 °C is it estimated to be only slightly higher (van Lenteren *et al*., 1996) so biological control should be possible under these conditions. But, van Roermund and van Lenteren (1992; 1995) showed that the *E. formosa* strain used in the Netherlands at that time did not fly at 18 °C or lower temperatures, which seriously lowers the parasitoid's dispersal and prevent whitefly patches from being found and parasitized. In Colombia, days are short when compared with the growing season in the temperate zones and the unheated greenhouses only warm up several hours after sunrise and cool down before sunset. The time that the conditions are optimal for foraging is therefore much shorter. Nevertheless, recent greenhouse trials showed that biological control of *T. vaporariorum* by *E. formosa* was possible in the specific greenhouse conditions on the Bogotá plateau (De Vis and van Lenteren, 2008).

A possible alternative to the biological control of *T. vaporariorum* by *E. formosa* is the native parasitoid *Amitus fuscipennis* MacGown and Nebeker (Hymenoptera Platygastridae). It can be found abundantly on field-grown tomato crops in Colombia, naturally parasitizing up to 80% of the *T. vaporariorum* pupae (De Vis and van Lenteren, 1999). Its life history as a parasitoid of *T. vaporariorum* was determined on bean (Manzano *et al.*, 2000) and on tomato (De Vis *et al.*, 2002). This re-

vealed that the intrinsic rate of increase of the parasitoid is substantially higher than that of *T. vaporariorum* between 15 and 30 °C, and slightly higher than that of *E. formosa* at temperatures lower than 30 °C. De Vis *et al.* (2003) found that *A. fuscipennis* had a higher searching efficiency resulting in a higher oviposition rate on tomato leaflets infested with *T. vaporariorum* larvae than that found by van Roermund and van Lenteren (1995) for *E. formosa*. These findings coincide with those of Manzano (2000) on bean. However, *A. fuscipennis* had a longer residence time on clean leaflets and a shorter longevity than *E. formosa*, and this might reduce its efficacy as parasitoid in crops with a low host density.

Interaction experiments between *E. formosa* and *A. fuscipennis* showed that both parasitoid species treated *T. vaporariorum* larvae parasitized by the other species in the same way as unparasitized larvae. Therefore, multiparasitism was frequently observed and in 70-80% of the cases, only the species that parasitized first emerged from multiparasitized whitefly larvae. Thus, neither species was observed to be superior to the other when internal competition for host possession occurred (De Vis *et al.*, 2003).

The two parasitoid species have a similar intrinsic rate of increase but different, possibly complementary, life history traits. The pro-ovigenic *A. fuscipennis* has a high egg load and high oviposition frequency (De Vis *et al.*, 2002), and could therefore prove to be good at reducing whiteflies in high-density spots. The synovigenic *E. formosa* acts also as a predator and needs host feeding for egg maturation. It can prolong its longevity through oosorption (Van Keymeulen and Degheele, 1978; van Lenteren *et al.*, 1987) resulting in a longer adult life. When hosts are continuously present, *E. formosa* can oviposit approximately 10-16 eggs per day during a period of 30 days or more. The life history strategy of *E. formosa* is thus more suited than that of *A. fuscipennis* to maintaining *T. vaporariorum* at low density during long periods. As a result of these different life history strategies, the joint use of both parasitoids in greenhouses might be more efficient than the use of a single parasitoid species.

In the experiments described in this paper, we evaluated *A. fuscipennis* used with or without *E. formosa* as biological control agent for the greenhouse whitefly on tomato under the specific greenhouse conditions of the Bogotá Plateau.

Materials and methods

Experimental greenhouses

Two tomato production cycles were conducted at the Horticultural Research Centre (CIAA) of the Jorge Tadeo Lozano University, 20 km north of Bogotá (2665 m altitude) in two types of unheated greenhouses. The first was a plastic greenhouse of the standard Colombian design (fixed open ridge and manual wall curtains) equipped with a thermal screen. The second was a "Dutch-Venlo" type glasshouse with automated roof ventilation, a thermal screen and computerized environmental control (Midi-Clima, Van Vliet, The Netherlands). The climate control of the glasshouse was programmed as to reach the highest possible mean temperature, respecting the optimal plant growth temperature and relative humidity zone, while temperature management in the plastic greenhouse was limited to manual opening of the wall curtains when temperature was to high and closing the thermal screen at night. The computer also recorded temperature in both greenhouses using NTC sensors installed in a ventilated box. Relative humidity was calculated using the temperature data from a dry and a wet sensor installed in the same box. The boxes were installed in the centre of each greenhouse at plant height and every ten minutes the mean value of the previous 10 minutes was stored. Tomato plants of the variety "Boris" (Bruinsma Seeds, 's-Gravenzande, The Netherlands) were transplanted in both greenhouses during two consecutive production cycles as follows: 1) 7-week old plants were transplanted on September 6, 1999 and production was terminated on March 12, 2000 during the first cycle; and 2) 6-week old plants were transplanted on March 30, 2000 and production was terminated on October 15, 2000 during the second cycle. Each production cycle, a total of 1152 plants (12 beds of two rows of 48 plants each) on an area of 510 m^2 (25 m by 20.4 m) were planted in the plastic greenhouse. In the glasshouse, 672 plants (6 beds of two rows of 56 plants each) were planted on an area of 273 m^2 (28 by 9.6 m). The experiments began during the week of transplant in the first and one week after transplant in the second trial. At that time, a natural infestation of *T. vaporariorum* adults was present in all experimental greenhouses. The census at the beginning of the experiments showed that the whitefly population was lower in the first than in the second experiment. In the first, 0.0016 and 0.0063 whitefly adults per plant were found in the glasshouse and the plastic greenhouse respectively, compared to 0.075 and 0.16 adults per plant in the second. These adults most likely survived from previous crops, because no significant immigration of *T. vaporariorum* adults could have taken place as outside temperatures were too low for *T. vaporariorum* population build-up. In the adjacent greenhouses, *T. vaporariorum* was controlled chemically or the crops in those greenhouses were not suitable for *T. vaporariorum* development.

Parasitoid release rates

A. fuscipennis was introduced during the first 13 weeks of production at a rate of 5 pupae per m^2 per week during the first trial. Both *A. fuscipennis* and *E. formosa* were introduced together during the first weeks of production during the second trial at a rate of 2.5 pupae each per m^2. A total of 65 parasitoids per m^2 were introduced in both trials. Pieces of leaflets with about 70 parasitized *T. vaporariorum* pupae were equally distributed throughout the greenhouses. They were fastened to the base of the lower leaves of the tomato plants. Mean emergence of the introduced pupae was 95% or higher. Parasitoids originated from the CIAA's rearing unit where they were reared on tomato plants.

Adult whitefly and parasitism monitoring

Whitefly adults were counted weekly on the 8 upper leaves of a stratified sample of 10% of the plants: within a row, of every ten consecutive plants, one was selected

at random. Eggenkamp-Rotteveel Mansveld *et al.* (1978) found that a stratified random sampling alone was not suitable to reliably estimate the total whitefly population in a large greenhouse. Therefore, we assessed the spatial distribution by censuring whiteflies every five weeks. To visualise the spatial distribution, greenhouses were divided in plots of 4 (2 x 2) plants and the mean number of whiteflies per plant of the plot was calculated based on the results of the whitely census done every five weeks. According to four density classes, two-dimensional maps were constructed.

Parasitism was assessed by weekly sampling of the parasitized and non-parasitized pupae on a stratified sample of 10% of the plants, one leaf per plant. Only leaves where some black pupae had already hatched were selected. On those leaves most of the non-parasitized pupae had already hatched. The number of parasitized pupae that were not yet black and thus counted as non-parasitized pupae was in this way reduced to a minimum. Sampling of week n + 1 was done on leaves that were located 2 to 3 leaves higher on the plant than the sampled leaves of week n. Percent parasitism was calculated as the sum of the parasitized pupae found on all plants on a sampling date divided by the total number of pupae.

During the first trial, plants with more than 100 whitefly adults were sprayed with buprofezin and thiociclam in the glasshouse in week 18 of the experiment. Powdery mildew and the disease caused by *Botrytis* were controlled with fenarimol and iprodione. Leafminers and aphids were kept at low densities by naturally occurring parasitoids during the two production cycles. The tomato russet mite, *Aculops lycopersici* (Tryon), was controlled mainly by spot treatments with fenbutatinoxide and occasionally a full crop treatment was necessary. All pesticides were supposed to be compatible with the application of *E. formosa* (table 1).

Results

The mean temperature and relative humidity (days as replicates) was significantly different among production cycles and greenhouses, except for the relative humidity, which was similar in the glasshouse and plastic greenhouse in the first trial (figure 1, A and B). The mean daily temperature curve of both greenhouses showed a small but consistent difference (showing the data of the first trial, figure 1C).

The *T. vaporariorum* adult population increased steadily in both greenhouses in first trial, but with a higher rate in the glasshouse. In the glasshouse, it reached 10 adults per plant by week 15, while this level was only reached by week 21 in the plastic greenhouse. After week 15 the difference between the two greenhouses increased, the population in the glasshouse being 2 to 4 times higher than in the plastic greenhouse. But by week 23, the population in the plastic greenhouse increased exponentially, reaching that of the glasshouse by week 24. The maximum *T. vaporariorum* adult population was nearly 50 adults per plant in both greenhouses (figure 2). At the beginning, parasitism was more than 80% in both greenhouses, but it fell below this level by week 13 in the glasshouse and by week 17 in the plastic greenhouse. It reached a minimum of 20% in the glasshouse by week 18 and a minimum of 48% by week 24 in the plastic greenhouse. After reaching this minimum it started to increase again to 70% by week 24 in the glasshouse (figure 3). Although *E. formosa* was not introduced in this trial, parasitism by this parasitoid was observed from the beginning of the experiment. Most of the time it caused between 10 and 20% of the total parasitism in the glasshouse, but from week 22 this increased to more than 50% by the end of the experiment. In the plastic greenhouse, parasitism caused by *E. formosa* was less than 10% up to week 17 of the experiment, and between 15 and 20% for the rest of the experiment (figure 4). The number of pupae per leaf increased slower in the plastic greenhouse than in the glasshouse. In the glasshouse, the level of 20 pupae per leaf (sum of parasitized and unparasitized pupae) was reached by week 20, but only by week 23 in the plastic greenhouse. A maximum of more than 120 pupae per leaf was found by week 24 in the glasshouse and more than 60 per leaf in the plastic greenhouse by week 25 (figure 5).

In the second trial, the *T. vaporariorum* population was under control in both greenhouses during the whole experiment. Most of the time it was below 0.5 adults per plant with a small increase in the population, up to 1.2

Table 1. Pesticides used during the trials and their compatibility with natural enemies. The value indicates the toxicity of the respective product according to the IOBC rating system where 1 = harmless or less than 25% mortality; 2 = slightly harmful, between 25 and 50% mortality; 3 = moderately harmful, between 50 and 75% mortality and 4 = very harmful, more than 75% mortality. The persistence of the product, in weeks, is given between brackets. When more than one figure is given, toxicity for the different natural enemies was different. A question mark indicates that no data are available.

Active ingredient	Trade name	*E. formosa*		Other parasitoids	Predators
		Adult	Pupa		
Buprofezin	Oportune	2 (0.5)	1	1 (0)	1, 2 (1)
Fenarimol	Rubigan	1 (0)	1	1 (0)	1 (0)
Fenbutatinhydroxide	Torque	1 (0)	1	1 (0)	1 (0)
Iprodione	Rovral	1 (0)	1	1 (0)	1 (0)
Thiocyclam hydrogen -oxalate	Evisect	1 (0)	4	1, 2, 3, 4 (?)	1, 2, 3, 4 (0, 1, 2)

Source: http//www.koppert.nl, Side effect database.

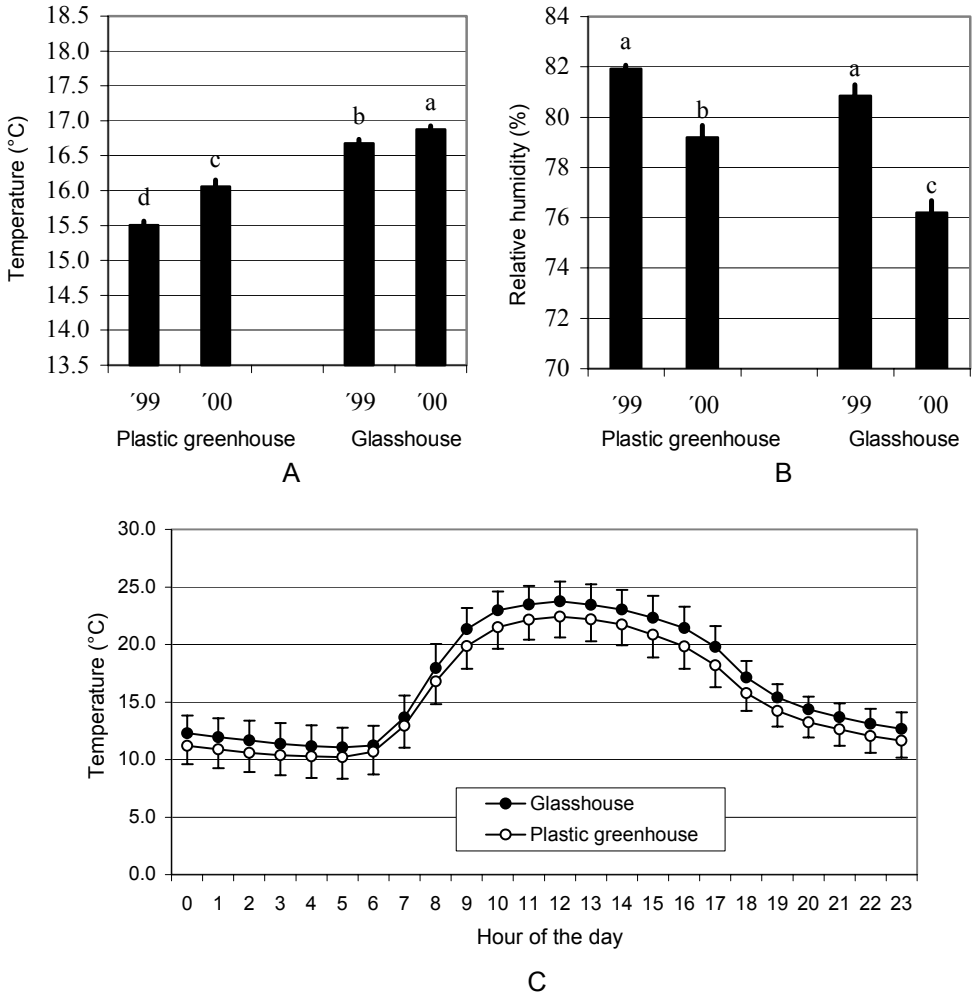

Figure 1. Mean temperature (A) and relative humidity (B) of the greenhouses during the two production cycles. Means with the same letter are not significantly different ($\alpha = 0.05$). Mean daily temperature curve of both greenhouses during the first production cycle (C).

adults per plant during weeks 12 to 16 of the experiment (figure 2). Parasitism was generally above 90%, with a small decrease during weeks 12-15, when it was still higher than 80% (figure 3). Parasitism was caused mainly by *E. formosa*. In the glasshouse, this parasitoid caused more than 80% of the total parasitism and from week 13 on, even 90% or more. In the plastic greenhouse, parasitism by *E. formosa* was lower at the beginning (51 and 67% in week 6 and 7 respectively), but by week 12 it was also above 90% and this level was maintained most of the time (figure 4). Less than 3 pupae per leaf (sum of parasitized and unparasitized pupae) were found in both greenhouses during the whole trial (figure 5).

The distribution maps of the first experiment (figures 6 and 7) show the very low initial infestation. Only one and seven infested squares were found in the glasshouse and the plastic greenhouse respectively. However, five weeks later, more than 50% of the squares were infested in both greenhouses. By week ten, the number of infested squares had decreased in the plastic greenhouse to 48% while in the plastic greenhouse only 3 uninfested squares were found and the first square with more than 10 *T. vaporariorum* adults per plant was found. From week 15 on, all squares were infested in both greenhouses and by week 25, several squares with more than 100 adults appeared. In the plastic greenhouse, the population was higher against the northern wall in weeks 5 and 15 and the eastern wall in week 20. In the glasshouse, the southern part had the highest *T. vaporariorum* population. In the second trial, the number of infested squares at the beginning was higher than in the first (figures 8 and 9). The number of infested squares in week 5 and 10 was lower than or similar to that in week 0 in both greenhouses. More infested squares were found in week 15 and 20 but the infestation level was lower than 10 adults per plant, except for one square in the glasshouse in week 15, and one in the plastic greenhouse in week 20. Patches separated by whitefly free zones did not develop, although plants without whiteflies were frequently observed alongside plants that were heavily infested.

Discussion

In first experiment, the *T. vaporariorum* adult population could not be kept under biological control in both greenhouses. In the plastic greenhouse, whitefly num-

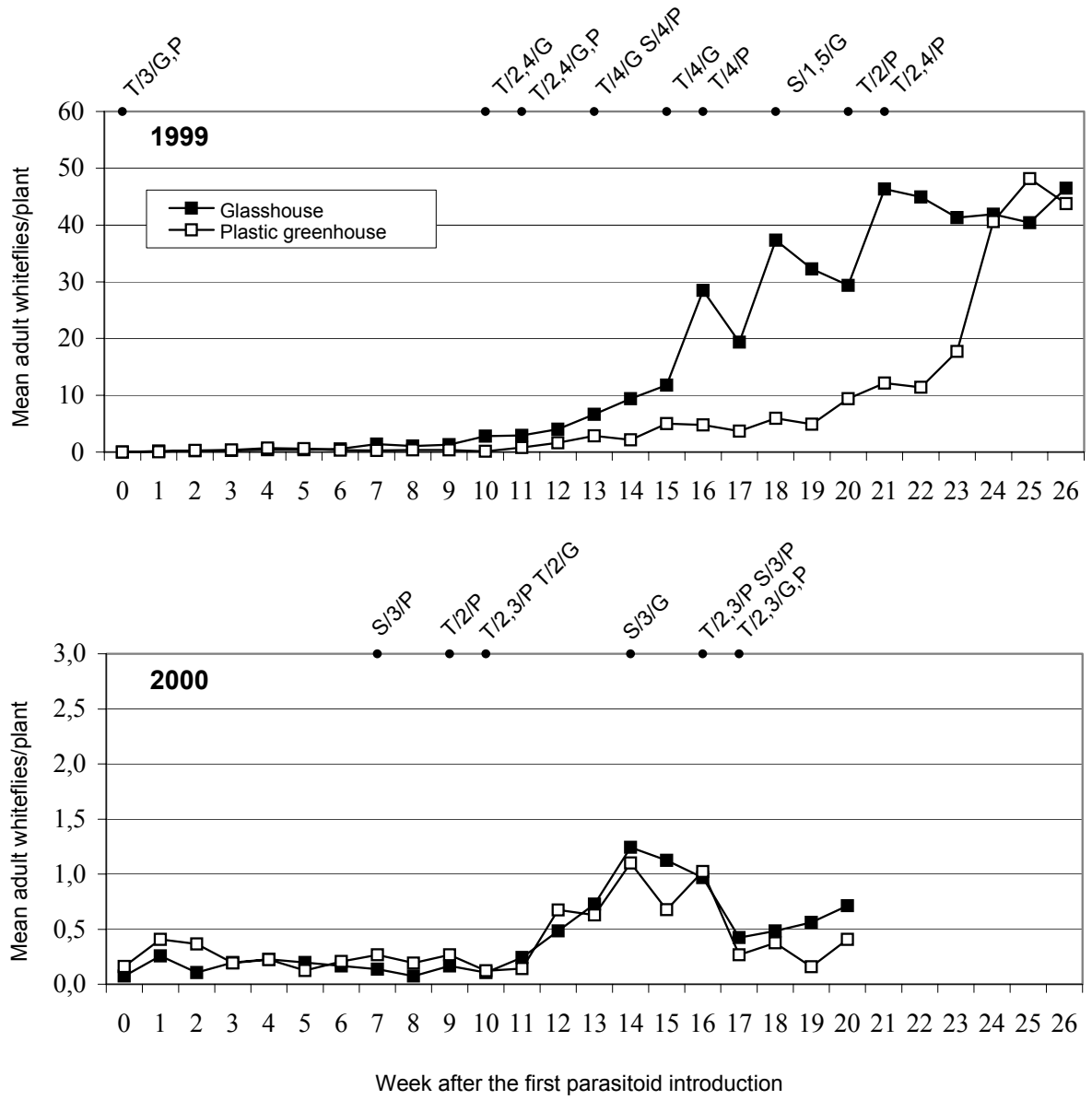

Figure 2. Mean number of adult whiteflies per plant in the glasshouse and in the plastic greenhouse during the two production cycles. The chemical treatments are specified above the graphs: S = spot treatment; T = total crop treatment; G = glasshouse; P = plastic greenhouse; 1 = buprofezin; 2 = fenarimol; 3 = fenbutatinoxide; 4 = iprodione; 5 = thiocyclam hydrogen oxalate. For the compatibility of the pesticides with *E. formosa* see table 1.

bers remained below the economic injury level (about 5 whitefly nymphs per cm^2 for tomatoes; Hussey *et al.*, 1958) until week 19. The total immature development time of *A. fuscipennis*, calculated with the equation presented in De Vis *et al*. (2002) and the hourly temperature data of the plastic greenhouse in the first trial was 48.1 days. Therefore, parasitoids that emerged in week 19 were the result of whiteflies that had been parasitized in week 12. As the *T. vaporariorum* population started to increase by week 19, parasitism in week 12 was apparently not sufficient. To estimate the number of emerging parasitoids per plant we multiplied the number of parasitized pupae per leaf by the estimated leaf initiation rate of 1.9 leaves per week (Jones *et al.*, 1991), resulting in 2.8, 5.5, 8.8, 10.4 and 15.4 emerging parasitoids per plant for weeks 12 to 16. During those weeks, the *T. vaporariorum* population increased from 1.6 to 5.0 adults per plant. The same calculations can be made for the glasshouse, where the *T. vaporariorum* population was under control for the first three months. Here, the total immature development time of *A. fuscipennis* was calculated to be 42.9 days. Therefore, pupae emerging in week 14 were parasitized in week 8. Calculated parasitoid emergence increased from 2.3 to 6.5 adults per week and per plant from week 9 to week 13. Together with the emergence of the introduced parasitoid pupae, the total emergence was estimated to increase from 4.3 to 8.5 parasitoids per week and per plant. Between weeks 8 to 13 the *T. vaporariorum* population was between 1.1 and 6.6 adults per plant. Thus, in the two situations the estimated adult parasitoid population was larger than the *T. vaporariorum* adult population. Additionally, longev-

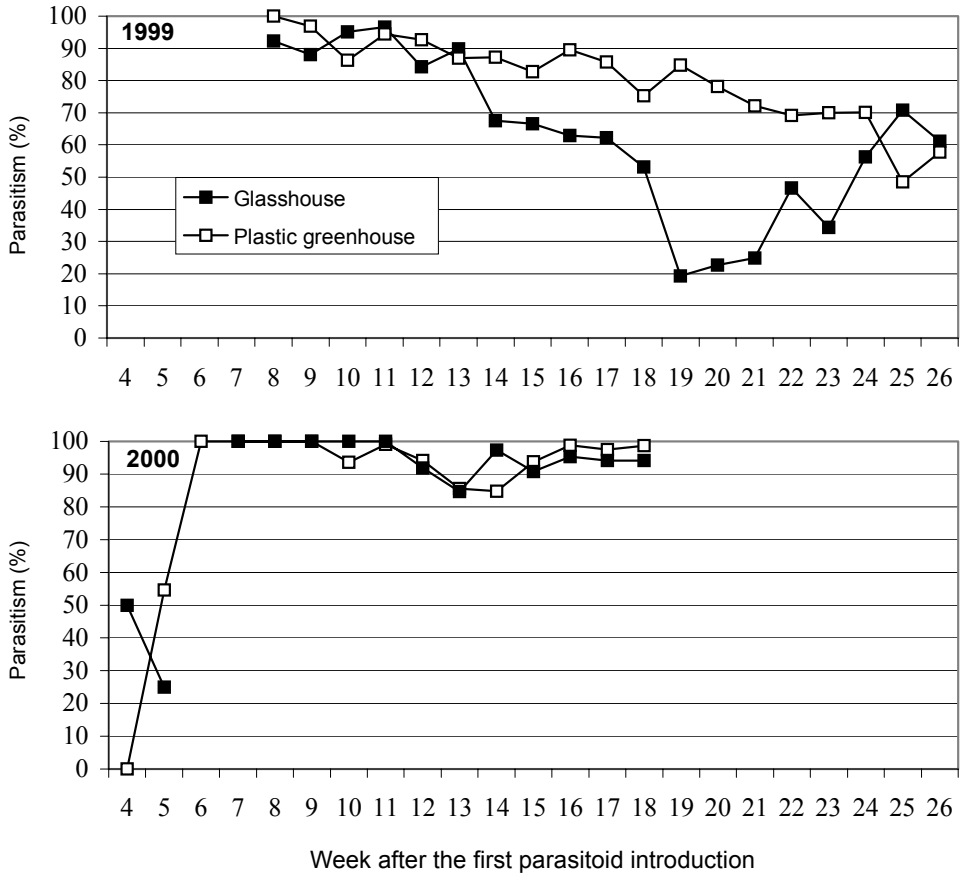

Figure 3. Percent parasitism in the plastic greenhouse and in the glasshouse during the two production cycles.

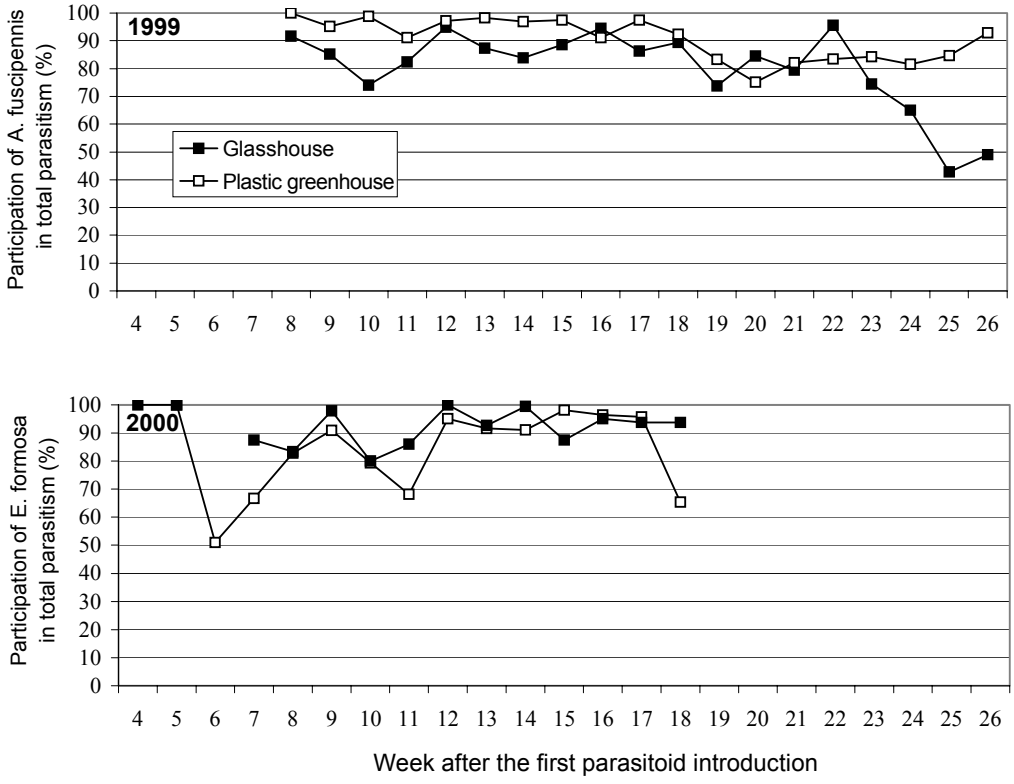

Figure 4. Participation of *A. fuscipennis* (first trial) and *E. formosa* (second trial) in total parasitism in the plastic greenhouse and in the glasshouse.

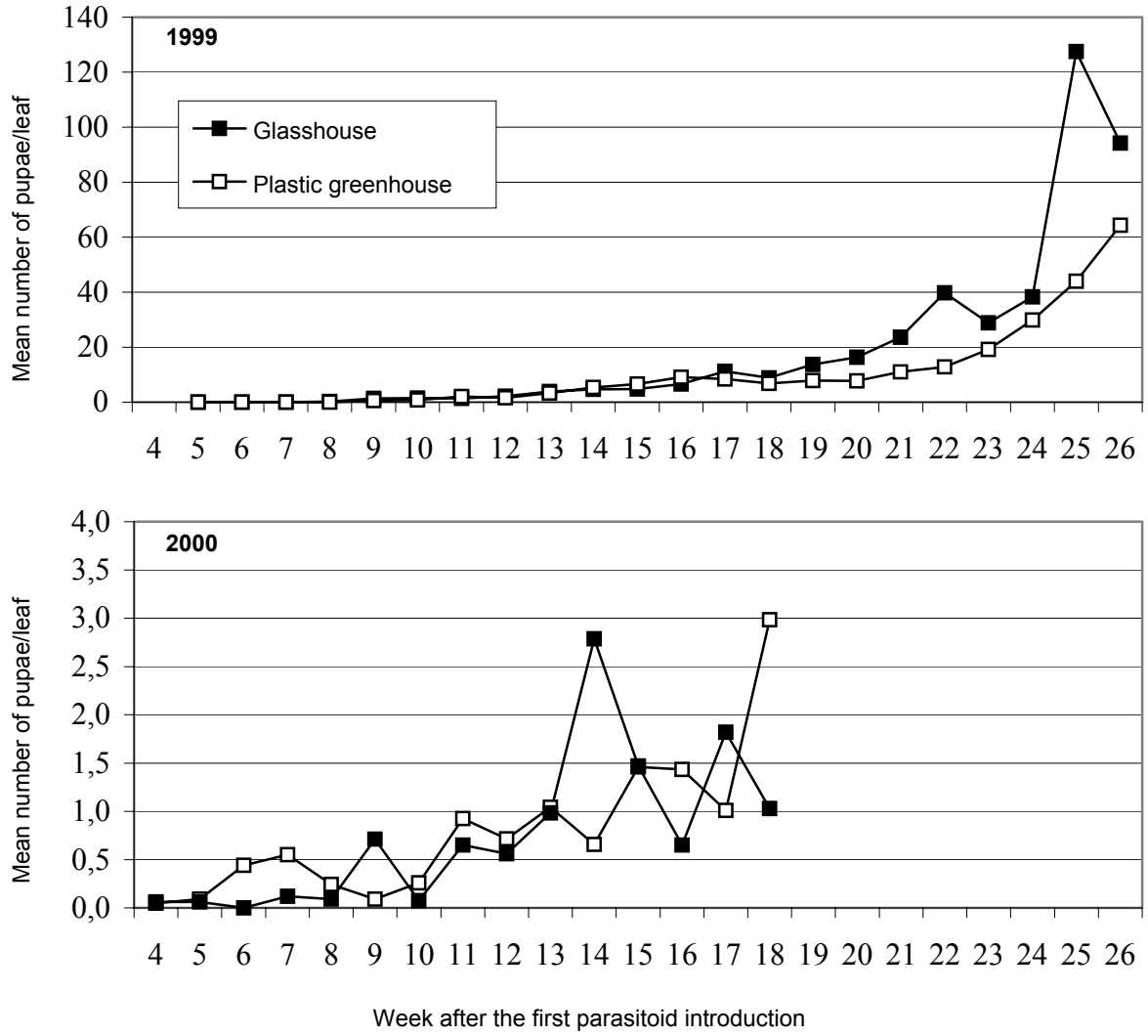

Figure 5. Mean total number of parasitized and unparasitized pupae per leaf in the plastic greenhouse and in the glasshouse during the two production cycles.

ity of *A. fuscipennis* at 15 °C was 18.1 days (De Vis *et al.*, 2002), so parasitoids of at least two weeks could have accumulated in the crop. Despite these high estimated numbers of parasitoids, *T. vaporariorum* populations were not controlled. There may be several explanations for this result:

1 During the weeks previous to the *T. vaporariorum* increase, chemical treatments were applied. This could have hampered emergence or killed adult *A. fuscipennis* resulting in a higher *T. vaporariorum* population in the next generation. During weeks 10 to 16 a total of four full crop sprayings were done in the glasshouse compared to only two in the plastic greenhouse. This can also explain why the *T. vaporariorum* population started to increase earlier in the glasshouse than in the plastic greenhouse. In previous trials, De Vis and van Lenteren (2008) found that pesticide applications could cause high mortality to *E. formosa* adults. It is not clear, however, if spraying or the chemical products we used affected *A. fuscipennis* more than *E. formosa* (table 1). At the moment, no data are available for the side effects of pesticides on *A. fuscipennis* adults or immatures.

2 The parasitoids may not have found the larvae in the extensive crop that had more than 20 leaf layers with up to 20 leaflets per leaf. *A. fuscipennis* females have an egg load of at least 430 eggs at emergence (De Vis *et al.*, 2002) and in the above section we estimated that the parasitoid population was larger than the *T. vaporariorum* population. Because fecundity of *T. vaporariorum* is lower than that of *A. fuscipennis*, the parasitoids were surely not egg limited. Rather, they were time limited in this crop with many leaves and leaflets. Still, with this high parasitoid-host ratio, we would expect a higher level of parasitism. Therefore, we conclude that the spraying caused high *A. fuscipennis* adult mortality.

3 During the last experiment many *A. fuscipennis* adults were found stuck to the glandular trichomes on the stems of the tomato plants, leading to mortality. However, we did not quantify this mortality and thus cannot estimate its impact on the success of biological control. In earlier work, we observed that *A. fuscipennis* females leave leaflets in most cases by

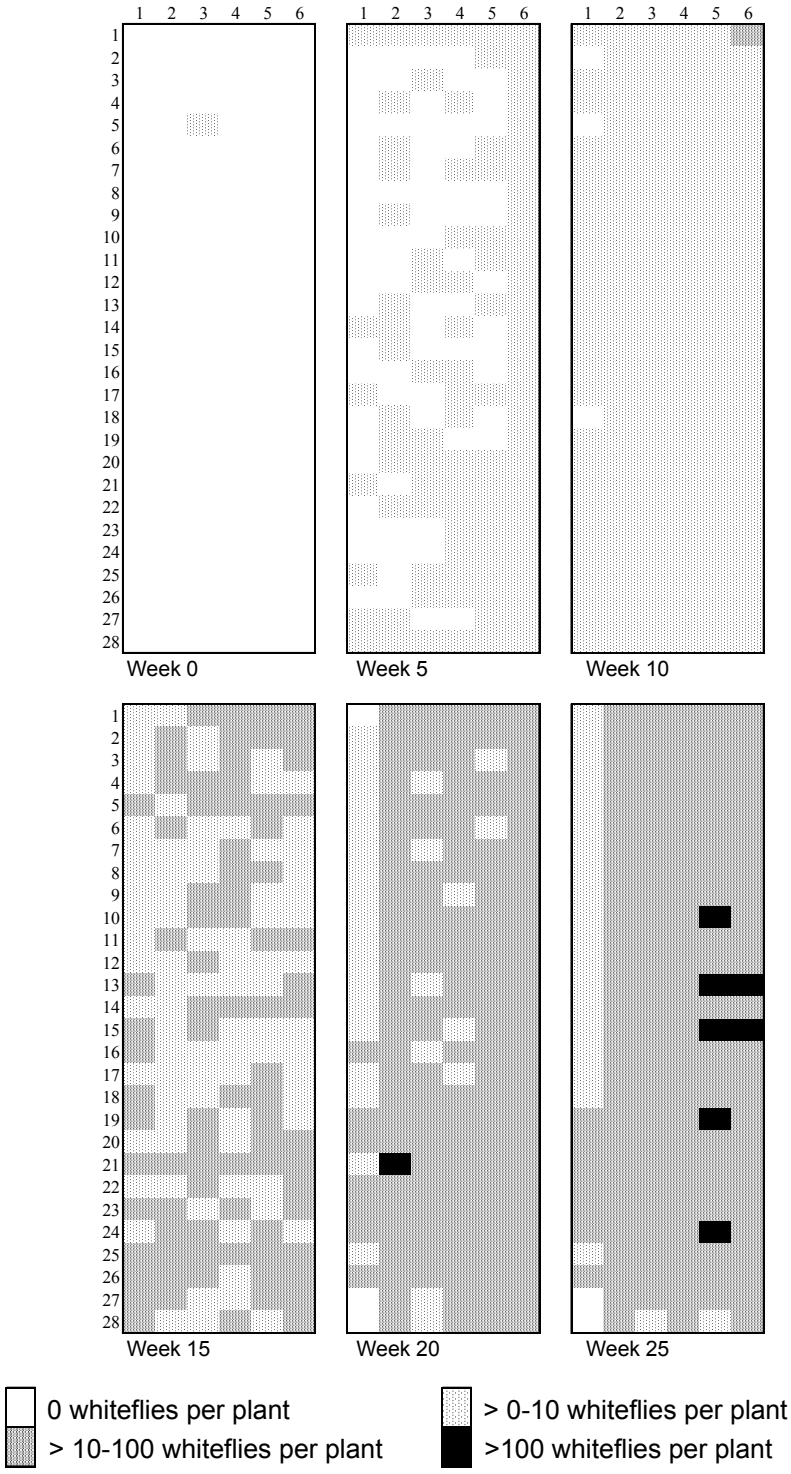

Figure 6. Spatial distribution of adult whiteflies in the first glasshouse trial. Each square represents four plants and the grey scale indicates the mean number of whitefly adults on the 8 upper leaves of the four plants. The week number indicates the number of weeks after the first parasitoid introduction.

walking via the petiole instead of flying (De Vis *et al.*, 2003). Manzano (2000) also observed that parasitoids move between leaflets by walking via petioles and stems. It seems that the glandular trichomes, which are present abundantly on tomato stems, are a mortal trap for these walking parasitoids. On tomato, this was also found for the predatory mite *Phytoseiulus persimilis* Athias-Henriot (e.g. Nihoul, 1994).

Because of the potential negative effect of sprayings, it is not clear whether the pro-ovigenic *A. fuscipennis* is capable of maintaining a *T. vaporariorum* population at low levels during the whole production cycle. Previous experiments where only *E. formosa* was used as biological control agent (De Vis and van Lenteren, 2008) showed that this parasitoid was able to maintain *T. vaporariorum* at low levels during a complete growing

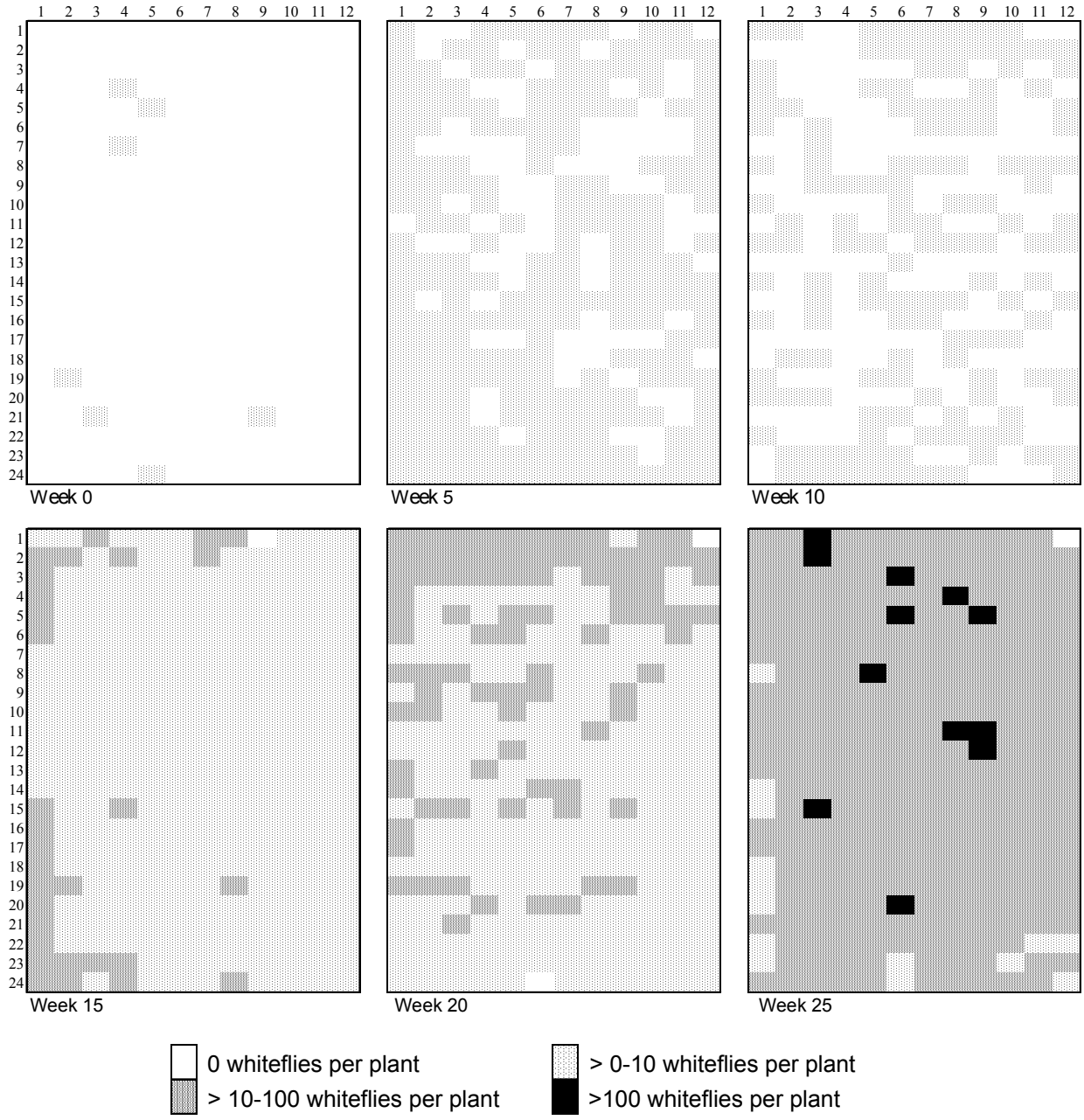

Figure 7. Spatial distribution of adult whiteflies in the first plastic greenhouse trial. Each square represents four plants and the grey scale indicates the mean number of whitefly adults on the 8 upper leaves of the four plants. The week number indicates the number of weeks after the first parasitoid introduction.

season of about 6 months and under the same growing conditions. However, when the number of full crop sprayings was high, *T. vaporariorum* population got also out of control with this parasitoid.

E. formosa possibly survived from the previous experiments (De Vis and van Lenteren, 2008) and contaminated the first experiment. Although not introduced, it established well in both greenhouses and counted for 50-60% of the parasitized pupae in the glasshouse at the end of the first trial. In the second trial, *E. formosa* caused more than 80% of the *T. vaporariorum* parasitism. Both results indicate that *E. formosa* is more efficient in controlling *T. vaporariorum* at low densities than *A. fuscipennis* under these circumstances. The searching efficiency of *A. fuscipennis* on infested leaflets is higher than that of *E. formosa* (De Vis *et al.*, 2003), but in crops with a low host density, parasitoids are searching most of the time on clean leaflets (van Roermund and van Lenteren, 1997). *E. formosa* stays only about half an hour on clean leaflets (van Roermund and van Lenteren, 1995) compared to about one hour for *A. fuscipennis* (De Vis *et al.*, 2003). Thus, at low host densities, *E. formosa* spends less time searching on the many empty leaves than *A. fuscipennis*. Furthermore, the longevity of *E. formosa* in the presence of hosts at 15 °C was 31 days (Burnett, 1949), which increased to 99.3 days in the absence of hosts but with a sugar diet (Vet and van Lenteren, 1981).

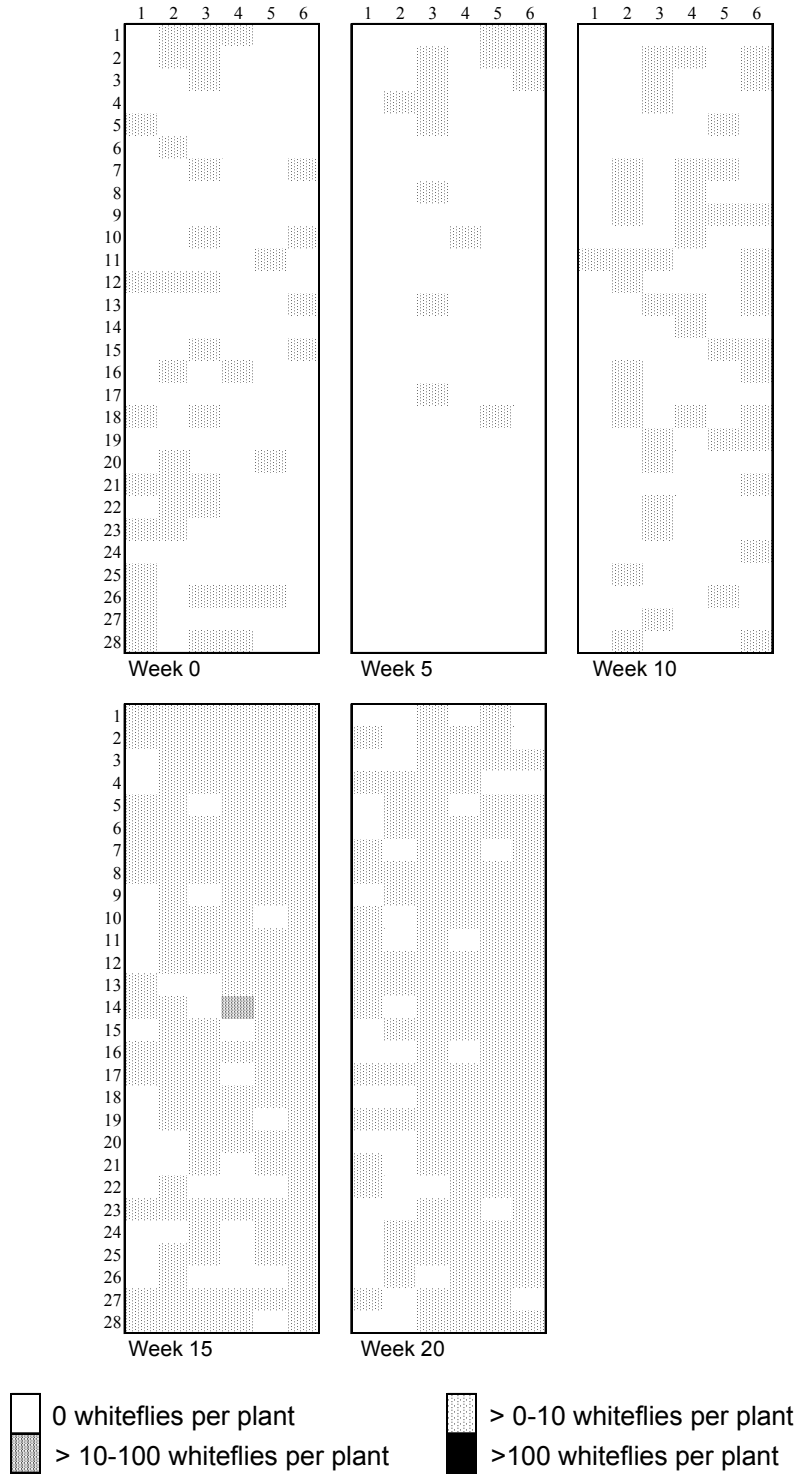

Figure 8. Spatial distribution of adult whiteflies in the glasshouse during the second trial. Every square represents four plants and the grey scale indicates the mean number of whitefly adults on the 8 upper leaves of the four plants. The week number indicates the number of weeks after the first parasitoid introduction.

For *A. fuscipennis* longevity was about 18 days under both conditions (De Vis *et al.*, 2002). Thus, because of the short residence time and the higher longevity, *E. formosa* will visit a considerably higher number of leaflets during its total life span than *A. fuscipennis*. This explains the higher parasitization efficiency of *E. formosa* when compared to *A. fuscipennis* in crops with low host density.

Examples of classical biological control programs where pro-ovigenic *Amitus* species were combined with synovigenic species seem to confirm our findings. *Aleurocanthus woglumi* Ashbi, the citrus blackfly was successfully controlled in Mexico and the USA by introducing 4 species of parasitoids: at the start of the introductions and when host density was very high, the pro-ovigenic *Amitus hesperidum* Silvestri was the dominant parasitoid, and

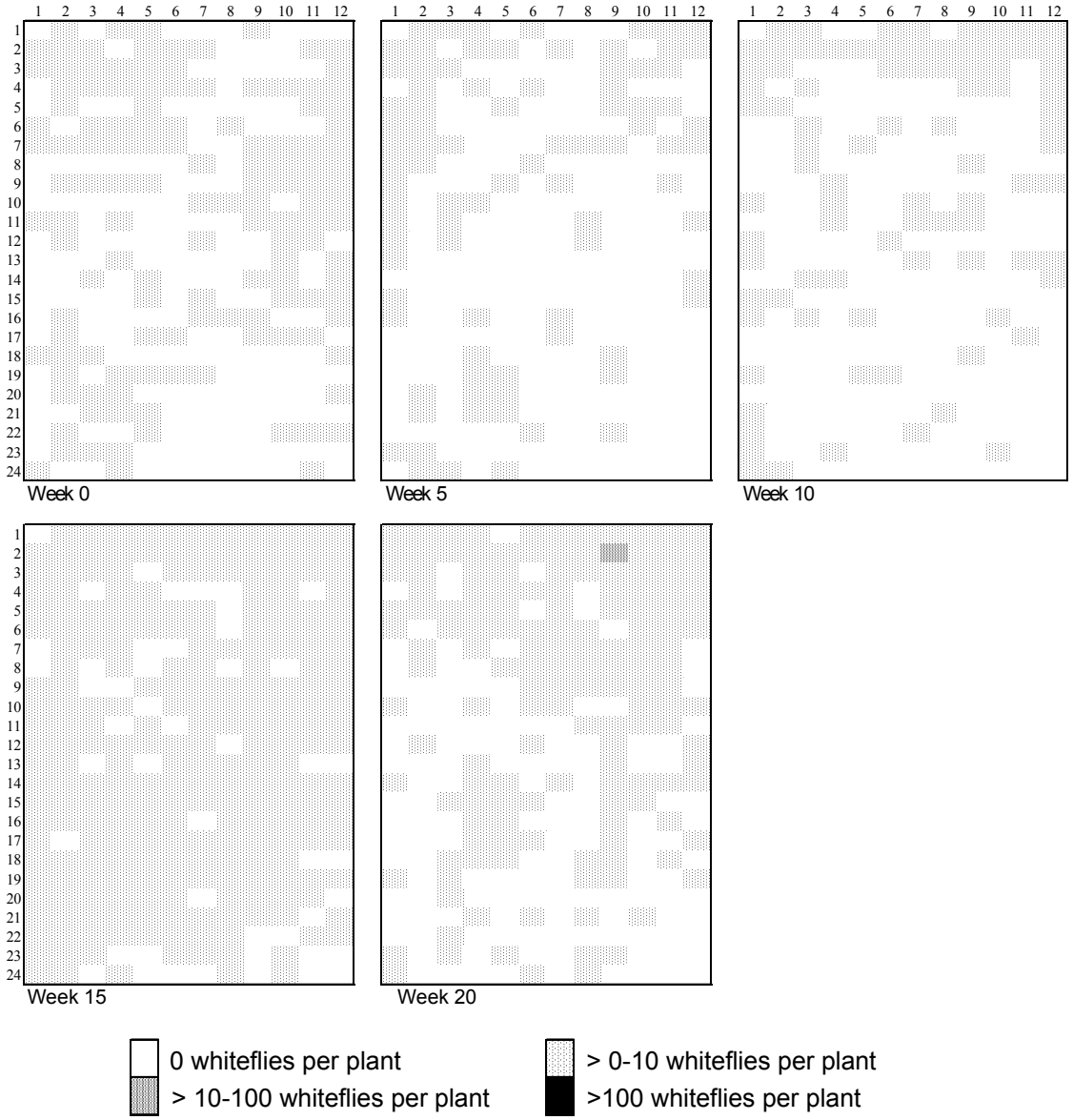

Figure 9. Spatial distribution of adult whiteflies in the plastic greenhouse during the second trial. Every square represents four plants and the grey scale indicates the mean number of whitefly adults on the 8 upper leaves of the four plants. The week number indicates the number of weeks after the first parasitoid introduction.

aphelinids like *Encarsia opulenta* (Silvestri) were hardly found. When host densities became low as a result of *A. hesperidum* parasitism, *E. opulenta* became the dominant parasitoid (Flanders, 1969; Dowell *et al*., 1981; Thompson *et al.*, 1987; Nguyen and Hamon, 1994). The woolly whitefly, *Aleurothrixus floccosus* (Maskell) was controlled in California by the introduction of an array of different parasitoid species and biotypes, including *Amitus spiniferus* (Brethes) and *Cales noacki* Howard. Also here, initially *A. spiniferus* reduced the high infestation levels within one year after the introduction and then *C. noacki* became the dominant parasitoid, which kept the population at low levels (DeBach and Rose, 1976). In these examples, the *Amitus* species disappeared almost completely after some years (Tsai and Steinberg, 1991; Thompson *et al.*, 1987; DeBach and Rose, 1976).

Examples where two synovigenic parasitoids are used have shown that this can lead to better control than the use of just one. *E. formosa* and *Eretmocerus eremicus* Rose et Zolnerowich are currently introduced together to control *T. vaporariorum* and *Bemisia* sp. in greenhouse tomatoes and ornamental crops. In this system, *E. formosa* is supposed to be more efficient at lower temperatures and lower host densities while *E. eremicus* is thought to be more efficient at higher temperatures and higher host densities (Koppert Biological Systems, M. Klein Beekman, personal communication). Further, Heinz and Nelson (1996) showed that the use of *Encarsia pergandiella* Howard or *E. formosa* alone led to poorer *Bemisia argentifolii* Bellows et Perring control than when both species were used.

Our greenhouse data do not provide evidence that the use of both *E. formosa* and *A. fuscipennis* leads to a better control than the use of one. However, the examples of *A. spiniferus* and *A. hesperidum* indicate that it might be

a good strategy to introduce both *A. fuscipennis* and *E. formosa* when many whiteflies are present. Also Drost *et al.* (1999) suggested that *Amitus bennetti* Viggiani et Evans might be a good parasitoid to quickly reduce high *B. argentifolii* populations while other parasitoids could then be used to keep populations low. The high control potential of *A. bennetti* was confirmed by Joyce and Bellows (2000) who found a percentage parasitism of 31, 40 days after releasing 300 *A. bennetti* in cages where 1500 *B. argentifolii* were released on 6 bean plants.

In conclusion, it is recommended to introduce both *E. formosa* and *A. fuscipennis* when the initial *T. vaporariorum* population is high or immigrations of whitefly are to be expected, but further research should confirm this. When the initial *T. vaporariorum* population is low it would be better to introduce only *E. formosa* and if a high-density spot develops or unexpected immigration occurs, *A. fuscipennis* can then still be introduced to reduce the *T. vaporariorum* population quickly. *E. formosa* can also be used in zones where *A. fuscipennis* is naturally present, as our data showed that control was successful when both species were used. To answer the question we posed at the outset, we can say that *A. fuscipennis* is not an alternative, but a promising addition to the biological control of *T. vaporariorum*.

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Authors' addresses: Raf M. J. DE VIS[1] (corresponding author, raf.de.vis@proefstation.be), Centro de Investigaciones y Asesorías Agroindustriales, Universidad de Bogotá Jorge Tadeo Lozano, Apartado Aéreo 140196 Chia, Cundinamarca, Colombia; Joop C. VAN LENTEREN (Joop.vanLenteren@wur.nl), Laboratory of Entomology, Wageningen University, P.O. Box 8031, 6700 EH Wageningen, The Netherlands.

[1] Current address: Research Station for Vegetable Production, Duffelsesteenweg 101, 2860 Sint-Katelijne-Waver, Belgium.

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