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BIOLOGICAL AND INTEGRATED CONTROL OF *FRANKLINIELLA OCCIDENTALIS* (PERGANDE) ON ORNAMENTALS IN THE NORTHEASTERN ITALY

Director of the School : Ch.mo Prof. Antonio Berti
Coordinator: Ch.mo Prof. Francesco Favaron
Supervisor: Ch.mo Prof. Carlo Duso

Ph.D. Candidate : Andrea Boaria

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Riassunto

Sono stati condotti esperimenti di laboratorio, semi-campo e campo (serra) volti a individuare strategie di lotta biologica ed integrata da applicare contro *Frankliniella occidentalis*. E' stata studiata la distribuzione spazio-temporale dei principali tripidi fitofagi delle serre e dei potenziali antagonisti in alcune serre caratterizzate da un diverso livello di aperture laterali e in un roseto a cielo aperto. Le popolazioni di *F. occidentalis* si sono aggregate all'interno delle serre, quelle di *Tabaci tabaci* sia all'interno sia all'esterno delle serre. I tripidi predatori appartenenti al genere *Aeolothrip*s sono risultati anch'essi aggregati fuori e dentro le serre mentre gli antocoridi del genere *Orius*, sono stati riscontrati soprattutto ai margini delle serre e nel roseto a cielo aperto. Sono state riscontrate associazioni tra le distribuzioni spaziali dei tripidi fitofagi e dei loro antagonisti naturali suggerendo un potenziale ruolo di questi ultimi quali fattori di regolazione. La seconda ricerca sperimentale è stata intrapresa con lo scopo di dimostrare che il grado di apertura delle serre verso l'ambiente esterno non implica un maggiore incremento delle problematiche correlate ai tripidi su colture ornamentali. La colonizzazione di *F. occidentalis* è risultata favorita dai collegamenti interni (tra serre e serre o spazi logistici) mentre quella di *T. tabaci* non è stata influenzata dalle aperture laterali delle serre. Al contrario, le aperture laterali sono apparse promuovere la colonizzazione degli antocoridi. Il terzo studio è stato condotto con l'obbiettivo di valutare l'impatto di alcuni agenti di controllo biologico su *F. occidentalis*. Gli acari predatori rilasciati sulla chioma hanno fornito un efficace controllo del fitofago, mentre i nematodi e gli acari predatori hanno ridotto le densità del fitofago nel suolo. Nel quarto esperimento, l'effetto di un ceppo fungino di *Beauveria bassiana* su *F. occidentalis* ha raggiunto i livelli più elevati quando l'esposizione topica è stata combinata con quella residuale.

Summary

Laboratory, semi-field and field experiments were conducted with the aim of identifying biological and integrated control strategies to be applied against *Frankliniella occidentalis*. We studied the spatial and temporal distribution of the main thrips pests in greenhouses and potential antagonists in some greenhouses characterized by a different level of lateral openings and a rose garden in the open. The populations of *F. occidentalis* were aggregated in greenhouses, those of *Thrips tabaci* both inside and outside of greenhouses. The thrips predators belonging to the genus *Aeolothrips* were also aggregated outside and inside the greenhouses whereas anthocorid of the genus *Orius*, were found mainly at the edge of the rose garden, greenhouses and in the open air. Associations were found between the spatial distributions of thrips pests and their natural enemies, suggesting a potential role of the latter as regulatory factors. The second experiment was planned to show that opening greenhouse structures are not automatically related to an increase in thrips problems on ornamental crops. *F. occidentalis* seemed to penetrate from the interior of the greenhouse complex and was advantaged by cultivation practices and the connection among greenhouses. Unlike, *T. tabaci*, did not appear to be influenced by lateral openings nor the position in the greenhouse. Lateral openings promoted the colonization by *Orius* spp. Contrary, the lateral openings appeared to promote the colonization of anthocorids. The third experimental study has been undertaken with the aim of evaluating the impact of some biological control agents (BCAs) on *Frankliniella occidentalis* population. Predatory mites released at canopy level have provided an effective control of thrips, whereas entomoparasitic nematodes and predatory mites have reduced the pest density at soil level. In the fourth experiment, the effect of a fungal strain of *Beauveria bassiana* on *F. occidentalis* reached the highest levels when residual and topical exposures were combined.

Chapter I

Introduction

Economic importance of thrips

Among 5500 well-described thrips species (Lewis, 1997), only 1% are considered to be serious crop pests (Morse and Hoddle, 2006). Some species are key pests of open field-growing vegetables, others infest protected crops especially economically important plants (Tommasini and Maini, 1995). Currently, the most important threating thrips species around the world are *Frankliniella occidentalis*, *Thrips tabaci*, *T. palmi* and *Scirtothrips dorsalis* (Mound, 2002; Morse and Hoddle, 2006).

The pest status, referred to their economic importance, relies mainly to their ability to cause serious damage to crops and, as a consequence, heavy yield losses (Schoonhoven and Pena, 1989; Shipp et *al*., 2000). In addition, some thrips are efficient vectors of some serious plant-destroying Tospoviruses disease (Vierbergen et *al*., 1995; Ulman et *al*., 1997; Reley et *al*., 2011).

The international trade of food-producing plants as well as ornamentals has contributed strongly to increase the geographical distribution of many exotic thrips pests (Kirk and Terry, 2003; Morse and Hoddle, 2006), leading worldwide growers to use insecticides. In turn, large use of insecticides has led to the development of resistant strains, especially under greenhouse conditions; in addition thrips have a short development contributing to increase resistance spread (Reitz, 2009). This is the case of *F. occidentalis*, which has proved to be resistant to a wide range of insecticides (Immaraju et *al*., 1992; Jensen, 2000; Bielza et *al*., 2007). Thrips can cause serious damage to cultivated crops and huge yield losses, especially in the greenhouse where tolerance to crop damage is extremely low (van Lenteren, 2000).

The insecticide pressure selects species that result to be pesticide-resistant, and negatively affect other herbivore thrips and natural enemies (Tabashnick, 1989; Howarth, 1991). Moreover, the greenhouse environment provides excellent opportunities for the survival and development of a pest, even during cold periods (van Lenteren, 2000); for thrips pests that do not undergo into reproductive diapause, such as *F. occidentalis*, feeding damage can be observed in all time of the year (van Lenteren, 2000).

Until 1980, *T. tabaci* was the most important thrips pest in many greenhouses and field crops, vegetables, ornamentals, fruit trees and weeds (Tommasini and Maini, 1995). Later, *F. occidentalis* has quickly replaced the former species, becoming the dominant species.

Greenhouse thrips attributes

Phytophagous thrips are among the most important insect pests of protected crops all over the world (Bakker and Sabelis, 1989; Gillespie, 1989; Robb, 1989; Tommasini and Maini, 1995; Childer and Achor, 1995). The main questions related to thrips infesting greenhouse crops concern their life-style strategy, morphology, biology, ecology, insecticide resistance and their ability to transmit Tospoviruses (Trichilo and Leigh, 1988; Immaraju et *al*., 1992; Tommasini and Maini, 1995; Ulman et *al*., 1997; Jensen, 2000; Broadbent et *al*., 2003; Kirk and Terry, 2003; Mound, 2005; Reitz, 2009; Steiner et *al*., 2011).

They are able to damage host plants leading to foliar deformation, discolouration and flower abortion largely due to injection of saliva (Tommasini and Maini, 1995). Even though most thrips are oligophagous (Mound, 2005; Morse and Hoddle, 2006), thrips infesting greenhouse cultivations can exhibit an extreme degree of polyphagy (Reitz, 2009) Polyphagous thrips species are more likely to be pest species than monophagous or oligophagous species (Lewis, 1997; Marullo, 2004a; Moritz et al., 2004; Mound, 2005). Both *F. occidentalis* and *T. tabaci* are highly polyphagous thrips species.

Thrips are small and tiny insects and habitually feed in hidden environments, such as crevices, developing flowers, etc. Especially for flower-dwelling thrips, such as *F. occidentalis*, *F. intonsa* and other species, their attraction to flowers, also unopened ones, may often result in the reduction of contact with insecticide sprays (Reitz, 2009) Moreover, behavioural resistance (comprising thigmotactic, thigmotropic and thigmokinetic behaviours) exhibited by thrips species can easily compromise the chemical control success (Reitz, 2009; Bielza, 2008; Cloyd, 2009). In addition, the cryptic nature of soil-dwelling pupae can exacerbate the insecticide resistance (Broadbent et al., 2003; Berndt et *al*., 2004).

Generally, indigenous thrips that colonize greenhouses are easily controlled by insecticides (Costello and Elliott, 1981; Annon, 1987; Lewis, 1997), even if the resistance of *T. tabaci* to insecticide has been reported (e.g. van Lenteren and Woets, 1988; Shipp et al., 1991; Shelton et al., 2003; Herron et *al*., 2008). Invasive species, especially *F. occidentalis*, have developed strains highly resistant to insecticides (Immaraju et al., 1992; Jensen, 2000, Bielza et al., 2007). Insecticide resistance mechanisms include glutathione-S-

transferase, P450-monoxygenase and esterases (Jensen, 2000; Espinosa et *al*., 2005; Bielza, 2008). The insecticide resistance is responsible for the increase of economic costs associated to thrips control (Kirk, 2002; Lewis, 1997).

F. occidentalis and *T. tabaci* are known to transmit tospoviruses in a persistent propagative manner (Ullman et *al*. 1997). Only larval instars can acquire the virus, whereas only adults can transmit the virus after a latent period (Wijkamp et *al*., 1996, Ullman et *al*., 1997, Whitfield et *al*., 2005; Persley et *al*., 2006). *F. occidentalis* is a vector of TSWV, TCV, INSV, GRV, CSNV (Wijkamp et *al*. 1995; Sakurai et *al*. 2004; Whitfield et *al*. 2005; Nagata et *al*. 2004; Riley, 2011). *T. tabaci* can be a vector of INSV, TSWV and TYFRV (Cortes et *al*. 1998, Hsu et *al*. 2010; Wijkamp et *al*. 1995; Golnaraghi et *al*. 2007). Tospovirus infection is known to induce a suite of symptoms on its host plants including leaf speckling, mottling, chlorotic, and necrotic lesions of various shapes, sunken spots, etches, ring spots, stunting, yellowing, and wilting (Riley et al., 2011).

Main greenhouse thrips pests

Modern greenhouses are subjected to invasion by indigenous thrips in most countries, and in temperate climates they are also highly susceptible to the introduction of alien pest species (Morison, 1957; Vierbergen, 1995). Indigenous thrips, including *Thrips tabaci*, *Heliothrips haemorrhoidalis*, *Dichromothrips* spp., *Pathenothrips drecanae*, *Hercinothrips spp*., are successfully controlled by pesticides. More recently some exotic thrips species have been reported in greenhouses, i.e. *Frankliniella occidentalis*, *Hercinothrips femoralis*, *Thrips fuscipennis*, *Thrips palmi*, *Scirtothrips dorsalis* and most of them are damaging pests (Jacobson 1997).

Frankliniella occidentalis

F. occidentalis is a nearctic species (e.g., Alaska, California, Mexico) (Bryan and Smith, 1956; Stannard, 1968). Since 1960s it has spread towards eastern countries of USA and in various continents (Broadbend et *al*., 1987). *F. occidentalis* has been detected for the first time in Europe in 1983 in North-European greenhouse on imported *Saintaulia ionantha* plants (van de Vrie, 1987; Tommasini and Maini, 1995). In Italy, *F. occidentalis* has been originally discovered in nursery-grown *Saintpaulia* in Liguria (Arzone et *al*., 1989;

Tommasini and Maini, 1995). Then, it spread in all regions of Italy.

F. occidentalis is a bisexual species. Males are usually smaller and paler than females (Kirk, 2002). Diploid females originated from fertilized eggs whereas haploid males originated from unfertilized eggs (Higgins, 1992; Kumm and Moritz, 2010). The post-embryonic development involves two active feeding larval stages (first instar larvae and second instar larvae), two non-feeding pupal stages (prepupae and pupae) and mature adults (Tommasini and Maini, 1995). Pupae represent the cryptic stages of this species, being soil-dwelling (Berndt, 2004; Ebssa et *al*., 2006). Pupation normally occurs in the soil, but in some plants they can undergo to molt in the open flowers (Fransen and Tolsma, 1992; Jacobson, 1997; Broadbent et *al*., 2003) depending on floral architecture and environmental conditions (Buitenhuis and Shipp, 2008; Steiner et al., 2011). Eggs are laid into the plant tissues (petals, fruit, leaf) (Tommasini and Maini, 1995). Feeding involve hidden parts of flowers and the underside of leaves (Brodsgaard, 1994; Cloyd, 2009; Reitz, 2009).

F. occidentalis prefer flowers where both females and males can feed on pollen (Trichilo and Leigh, 1988), which can stimulate fecundity (Hulshof and Vanninen, 2002; Hulshof et *al*., 2003). *F. occidentalis* is also able to prey upon spider mites' eggs (Trichilo and Leigh, 1986; Pickett et *al*., 1988), being a facultative predator (Wilson et *al*. 1996; Mound 2005).

In the Mediterranean regions is usually found in greenhouses, where continuous generations take place during year-round (Broadsgaard 1989a; Parrella and Murphy).

Thrips tabaci

T. tabaci is a cosmopolitan and highly polyphagous thrips species, native to the eastern Mediterranean basin (Mound, 1983; Atakan et *al*., 2005). *T. tabaci* reproduces by constant thelitokous parthenogenesis (Tommasini and Maini, 1995). Developmental cycle comprises two immature larvae, two non-feeding immatures (prepupae and pupae) and adults. Females lay their eggs into plant tissues (Sakimura, 1932; Trdan et *al*., 2005a). Pupation occurs in the soil or humus around the host-plant (Tommasini and Maini, 1995). It usually attacks plants belonging to Liliaceae, some of economic importance (onion, leek, etc.) (Doederlein and Sites, 1993), but can infest about 300 plant species including several

ornamentals (Tommasini and Maini, 1995).

Integrated Thrips Management

The monitoring of thrips population is critical for successful pest management. The use of yellow and blue sticky traps is a basic method to monitor thrips population in the greenhouse environment, to identify the thrips involved, and to determine the critical location at risk (Brodsgaard, 1993; Kirk, 1984; Vernon and Gillespie, 1995; Shipp and Zariffa, 1991; Poncet et al., 2010).

Sanitation can implement pest management program (Jacobson, 1997). Flower removal can significantly reduce thrips populations. Cultural control measures also include maintaining a healthy crop and an optimal greenhouse environment that would provide less favourable conditions for a rapid increase in population densities. Use of thrips resistant cultivars is an important step within cultural measures (Mollema et al., 1993; Jacobson, 1997).

Concerning physical control, the insect exclusion screening restricts the movement into the greenhouse of many common greenhouse crop pests including thrips (Berlinger et al., 1991, 1993; Jacobson, 1997).

Chemical control is based on the use of insecticides with low persistence (Jacobson, 1997). Great attention is given to insecticides that are highly selective and harmless to non-target arthropods such as natural enemies (Jacobson, 1997). The rotation of different insecticide classes is crucial to reduce resistance risks (Lewis, 1997; Bielza, 2008; Cloyd, 2009).

Biological control is a key pillar in the integrated control of thrips (van Lenteren and Woets, 1988; Riudavets, 1995; Lewis, 1997; Cloyd, 2009). It relies to the use of well-known beneficial arthropods (predators, entomopathogens, entomoparasitic organisms). Some important organisms used in the biological control of thrips in greenhouses are predatory mites such as *Neoseiulus cucumeris*, *Amblyseius swirskii*, *Hypoaspis miles*, *H. aculeifer*, predatory bugs such as *Orius laevigatus*, *O. insidiosus*, *O. majusculus*, pathogenic fungi such as *Beauveria bassiana*, *Lecanicillium lecanii*, *Metarhizium anisopliae* and the nematode *Steinernema feltiae* (van de Veire and Degheeel, 1992; Chambers et *al*., 1993; Vestergaard et *al*., 1995; Jacobson et *al*., 2001; Berndt et *al*., 2004;

Messelink et al., 2006; Ansari et *al*., 2008; Tavella et *al*., 2008; Boaria et *a*l., 2011, 2013). Many studies showed the capacity of various BCAs to control thrips in greenhouses on cyclamen (de Courcy Williams, 2001; Boaria et *al*., 2013), sweet pepper (Jacobson, 1997; van de Veire and Degheele, 1992; Chambers et *al*., 1993; Tavella et al., 1996), cucumber (Jacobson, 1995, 1997), on flowering plants (Ravensberg and Altena, 1993; de Courcy Williams, 2001).

Thrips pest management in protected ornamentals is quite difficult when an environmentally-sound approach is required. In this work we investigated the interactions between herbivore thrips and their antagonists through laboratory, semi-field and field studies. Special attention has been given to greenhouse structures to look at possible measures to enhance conservative biological control in commercial greenhouses.

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Chapter II

Spatial and temporal distribution patterns of thrips and their natural enemies on protected ornamentals in northern Italy

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The manuscript in preparation as:

Andrea Boaria, Alberto Pozzebon, Carlo Duso – Spatial and temporal distribution patterns of thrips and their natural enemies on protected ornamentals in northern Italy

In this work, I collected most of the data, contributed to the analysis and drafted the manuscript

Abstract

Problems with herbivore thrips are commonly recorded on protected ornamentals. Failures in insecticide use to control these pests are reported because of their resistance. Alternative control strategies are based mainly on augmentative biological control (e.g. the release of predators) and the use of bio-insecticides. Conservation biological control is often overlooked in ornamental crop systems. Moreover, houses are planned to reduce arthropod exchanges from their surroundings because this is considered to enhance the colonization by herbivore thrips and other pests. In particular, houses devoted to ornamentals are opened only at the roof when temperatures exceed critical values. In this work, spatial and temporal dynamics of thrips pests and their potential natural enemies were investigated in a farm comprising houses characterised by an increasing level of lateral openings and an open field nursery. Investigations involved house and nursery surroundings, mainly hedgerows, small vineyards and orchards. Aggregation of the main species and the association between predators and prey were calculated using Spatial Analysis by Distance Indices (SADIE). The distribution of *F. occidentalis* population was commonly aggregated inside the houses while that of *Thrips tabaci* involved both the houses and their surroundings. Among natural enemies, predatory thrips (*Aeolothrips* spp.) evidenced an aggregated distribution both in greenhouses and outdoor, whereas anthocorids (*Orius* spp.) occurred most frequently in the surroundings of house or in the open field nursery. SADIE analysis revealed significant spatial associations between herbivore thrips and their natural enemies. Results and their relevance to Integrated Pest Management (IPM) are discussed.

Introduction

Herbivore thrips are major pests of protected ornamentals. *Frankliniella occidentalis* Pergande, also named Western Flower Thrips, causes serious economic damage by feeding on leaves and flowers (Brodsgaard, 1989a; Gerin et *al*., 1994; Helyer et *al*., 1995; Tommasini and Maini, 1995; Parrella and Murphy, 1996; Lewis, 1997a; van Dijken et *al*., 1994; Childers and Anchor, 1995) and transmits numerous Tospoviruses (Wijkamp et *al*. 1995; Ullman et *al*., 1997; CABI/EPPO, 1997). In greenhouses, WFT can develop and reproduce continuously due to optimal environmental conditions. Problems in successfully

managing this pest are because of its cryptic behaviour and resistance to insecticides (Lewis, 1997b; Jensen, 2000).

Thrips tabaci is a highly polyphagous and cosmopolitan thrips species (Lewis, 1973; Murai, 2000) that can be recorded in open-field and protected vegetables and ornamentals (MacIntyre Allen et *al*., 2005; Martin et *al*., 2003; Wimmer et *al*., 2008; Nault and Shelton, 2010; Mautino et *al*., 2013). It is able to transmit a number of viruses (Hardly and Teakle, 1992; Wijkamp et *al*., 1995, Murai, 2000; Gent et *al*., 2006; Nagata et *al*., 1999; Pappu et *al*., 2009). Resistance to pesticides is also known for this species (Martin et *al*., 2013; Nault et *al*., 2006; Shelton et *al*., 2006).

Problems encountered in the control of herbivore thrips have promoted a number of studies in the field of biological control, and the impact of various biocontrol agents as well as pathogens have been evaluated at different scales (Gillespie and Quiring, 1990; Brodsgaard, 1996; Jacobson, 1997; Baez et al., 2004; Brodsgaard, 2004; Buitenhuis and Shipp, 2005; Arthurs and Heinz, 2006; Ugine et *al*., 2005a, b; Boaria et *al*., 2011; Boaria et *al*., 2013). Some biocontrol agents proved to be effective against first instars less frequently on other life stages (van Lenteren and Woets, 1988; Shipp et *al*., 1991; van Houten et *al*., 1995; Messelink et *al*., 2005); however chemical control applied against other pests can disrupt the establishment of natural or artificially released beneficials (Higgins, 1992). As a consequence, biological control is often overlooked in protected ornamentals.

Relationships between pests and their natural enemies are influenced by the environment located at crop margins (e.g., Landis *et al.*, 2000; Marshall & Moonen, 2002). Biodiversity may represent an important resource for the management of thrips pests in greenhouses. Arthropod exchanges between natural and cultivated areas have been widely recognized as characterizing the population dynamics of pests and natural enemies in agroecosystems (Duelli et *al*., 1990; Marshall and Moonen, 2002; Macfadyen and Muller, 2013). Natural vegetation at the margin of greenhouses may represent a potential ecological corridor and a source of natural enemies potentially useful inside greenhouses. Concerning herbivore thrips, some studies have documented the ability of predatory bugs (e.g., *Orius insidiosus*) to colonize *F. occidentalis*-infested field pepper crops (Funderburk et *al*., 2000; Reitz et *al*., 2003). The colonization of greenhouses by these thrips antagonists has been reported by Tavella et *al*. (1996), Bosco et *al*. (2008), and Albajes and Alomar (1999). Arthropods

exchanges between greenhouses and their surroundings have been shown in open greenhouses in the Mediterranean climate. The predatory mite *Phytoseiulus persimilis* (Athias-Henriot) native to Mediterranean basin can colonize protected vegetables coming from outside and exert a fundamental role in controlling spider mite *Tetranychus urticae* Koch (Vacante and Nucifora, 1987).

Further case studies concerned whiteflies. Mediterranean predatory bugs such as *Macrolophus caliginosus* and *Dicyphus tamanini*, recognized as important whiteflies predators, naturally colonized protected and open field vegetables in Southern Italy and Spain (Vacante and Tropea Garzia, 1994; Riudavets and Castañé, 1998; Albajes and Alomar, 1999; Alomar et *al*., 2002; Lucas and Alomar, 2002; Castañé et *al*., 2004). Greenhouse structure may also strongly influence pests and natural enemies spatial dynamics between inside and outside greenhouse, contributing positively or negatively to their movements and therefore, to their distribution over the greenhouse and its surroundings (Albajes et *al*., 1999; Gabarra et al., 2004; Rich et *al*., 2013).

Greenhouses devoted to ornamentals are usually close environments. In summer, they are opened at the roof when temperatures exceed critical values. Moreover, growers eliminate accurately the vegetation surrounding greenhouses trying to create an artificial scenario where arthropod exchanges with outside environment are drastically reduced.

Studies of within-greenhouse spatial distribution of pests could help in managing them. Thrips have received a special attention at this regard (Higgins, 1992; Salguero et *al*., 1994; Cho et *al*., 1995; Cho et *al*., 2000; Cho et *al*., 2001; Deligeorgidis et *al*., 2002; Seal et *al*., 2006; Navarro-Campos et *al*., 2011). The spatial distribution analysis of *F. occidentalis* and *T. tabaci* infesting vegetables in both open field and greenhouses has been widely explored (Shipp and Zariffa, 1991; Higgins, 1992; Deligeorgidis et *al*., 2001; Pearsal and Myers, 2001; Cho et *al*. 2001; MacIntyre-Allen et *al*., 2005; Park et *al*., 2009; Poncet et *al*., 2010; Sedaratian et *al*., 2010). Research on protected ornamentals regarding natural enemies of pests has been less explored.

Several beneficial organisms can control thrips populations on different crops (e.g., Schreuder and Ramakers, 1989; Tavella et *al*., 1991; Jacobson, 1993; 2000; Tavella, 2000, 2003; De Courcy Williams, 2001; Jacobson et *al*., 2001; Deligeorgidis, 2002; Arthurs and Heinz, 2006; Ebssa et *al*., 2006). Among them, minute pirate bugs (*Orius* spp.), predatory

mites (*Amblyseius* spp., *Neoseiulus* spp., *Euseius* spp., *Hypoaspis* spp.) and predatory thrips (*Aeolothrips* spp.) have been reported as effective predators of *F. occidentalis* and *T. tabaci* (Bournier, 1968; Ferrari, 1980; Lacasa, 1980; Backer, 1988; Ananthakrishnan and Sureshkumar, 1985; Fischer et *al*., 1992; Riudavets et *al*., 1993; Tommasini and Nicoli, 1993; De Courcy Williams, 2001; Messelink et *al*., 2006; Wimmer et *al*., 2008; Conti, 2009). The role of *Orius* spp. in controlling thrips has been widely documented in open fields as well as in greenhouses (van de Veire and Degheele, 1992; Chambers et *al*., 1993; Tavella et *al*., 1996; Funderburk et *al*., 2000; Ramachandran et *al*., 2001; Blaeser et *al*., 2004; Bosco et al., 2008). Predatory mites belonging to the Phytoseiidae family, in particular *Amblyseius swirskii* and *Neoseiulus cucumeris*, are being widely employed for controlling thrips in greenhouses (Jacobson et *al*., 2001a, b; Messelink et *al*. 2006). Predatory thrips belonging to the genus *Aeolothrips* and *Franklinothrips* are commonly associated with phytophagous thrips, but their potential as biocontrol agents in greenhouses has been poorly investigated (Trdan et *al*., 2005; Cox et *al*., 2006; Fathi et *al*., 2008; Nammour et *al*., 2008; Pizzol et *al*., 2012).

The identification and evaluation of natural associations between indigenous crop pests and natural enemies are crucial in understanding the potential role of natural ecosystem as regulating factor of introduced exotic pest populations. The study of potential endemic natural enemies of an introduced exotic herbivore can therefore contribute to produce new noteworthy biological control results (van Lenteren, 1997) and to improve the knowledge on both the field-scale and small-scale level available existing regulatory services provided by natural and managed ecosystems.

Natural colonization of protected crops from uncultivated wild plants or other cropping systems by phytophagous thrips, as well as predaceous insects, in particular anthocorids and Aeolothripids, has been documented (van de Veire and Degheele, 1992; Tavella et *al*., 1996). However, the interaction between outside and inside greenhouse as well as the colonization potential of natural enemies is being poorly studied (Castane et *al*., 2004; Gabarra et *al*., 2004; Alomar et *al*., 2002; Bosco *et al.*, 2008; Atakan, 2010).

Some studies have been focused on the potentiality of natural environment to affect the populations of herbivores insects and their natural enemies by providing alternative food as well as site for mating, overwintering and shelter (Landis et *al*., 2000; Marshall and

Moonen, 2002; Frank and Reichhart, 2004; Gurr et *al*., 2005). Positive implications for sustainable thrips management on protected crops can result from flowering field margins or natural vegetation (van de Veire and Degheele, 1992; Perdikis et *al*., 2008; Atakan, 2010).

Some studies have been devoted to studying spatio-temporal distribution of WFT and *T. tabaci* on greenhouses and open field-growing vegetables (Higgins, 1992; Cho et *al*., 1995; Deligeorgidis et *al*., 2002). Pizzol et *al*. (2010) reported the use of glue sticky traps as an easy monitoring technique to successfully estimate thrips population on protected roses. Comparative studies on herbivore thrips and their natural enemies are lacking.

The spatial and temporal dynamics of thrips pests and their potential natural enemies were investigated in a farm comprising houses characterised by an increasing level of lateral openings and an open field nursery. Investigations involved house and nursery surroundings, mainly hedgerows, small vineyards and orchards. Aggregation of the main species and the association between predators and prey were calculated. Results are discussed for their relevance to Integrated Pest Management (IPM).

Materials and Methods

Study system

This study was conducted from 2011 to 2013 in a farm comprising several greenhouses (approx. 170000 m^2) devoted to the production of more than 200 plant species and located in northern Italy (Veneto region). The spatial and temporal distribution of thrips and their naturally occurring antagonists was investigated in three greenhouses where ornamentals and to a lesser extent vegetables were cultivated. An open field nursery where roses were grown was also considered in this comparison. The four cultivation scenarios had the following characteristics: 1) greenhouse (GH1) rectangular-shaped (5600 m^2) with four sides closed and facing a hedgerow in the northern side (H1) 2) greenhouse (GH2) rectangular shaped (4000 m^2) with a lateral opening on the northern side facing to a hedgerow (H2), and protected by an anti-lepidopteran plastic net (0.6 x 0.3 cm); 3) greenhouse (GH3) rectangular shaped (15000 m^2) with three lateral openings protected by anti-lepidopteran nets: the western side faced to a hedgerow (H3), the southern side to a

fruit orchard, the northern side to a vineyard and a greenhouse (north-eastern corner), the eastern side was close to other greenhouses; 4) an open field rose nursery (OFN) of about 5400 m^2 with the northern side facing to a secondary hedgerow (H4). Usual cultivation practices were adopted, and insecticides were applied every 15-20 days in houses less commonly in the open field nursery (Table 1). Three out of four hedgerows (H1, H2, H4) were established in 2011 to investigate on their potential role in increasing the colonization by natural enemies of pests (Bugg et *al*., 1989; Maingay et *al*., 1991; Patt et al., 1997). Plant species (e.g., *Lagerstroemia indica* L., *Lavandula* spp., *Viburnum opolus* L., *Corylus avellana* L., *Sambucus nigra* L.) were selected for this purpose based on data reported in the literature. The fourth hedgerow comprised some naturally occurring plants such as *Sambucus nigra* L., *Acer saccharinum* L., *Robinia pseudoacacia* L., *Phyllostachys mitis* (Poir.) Rivier et C. Rivière, *Carpinus betulus* L. and *Corylus avellana* L..

Observations were carried out from April to October in 2012 and 2013. Phytophagous thrips and their potential antagonists were captured by using 15 x 15 cm light yellow and blue glue sticky traps positioned in the greenhouses in regular grid of 10 x 10 m and following a *staggered design.* Sticky traps were also placed at the greenhouse margins comprised the hedgerows. Furthermore, sticky traps were placed at the roof of greenhouses and in the crop-free area in order to evaluate insect occurrence in absence of growing plants. Sticky traps were placed according to West-East direction and cards were fastened to 50 cm tall plastic stakes. Traps were initially placed 10 cm above the growing crops and raised even with the top of the canopy as plants grew. They were renewed at weekly intervals and analysed under a dissecting stereomicroscope. Thrips specimens were mounted on slides and identified using an identification key guide (Marullo, 1993; Mound and Kibby, 1998; Moritz and Goldarazena, 2004).

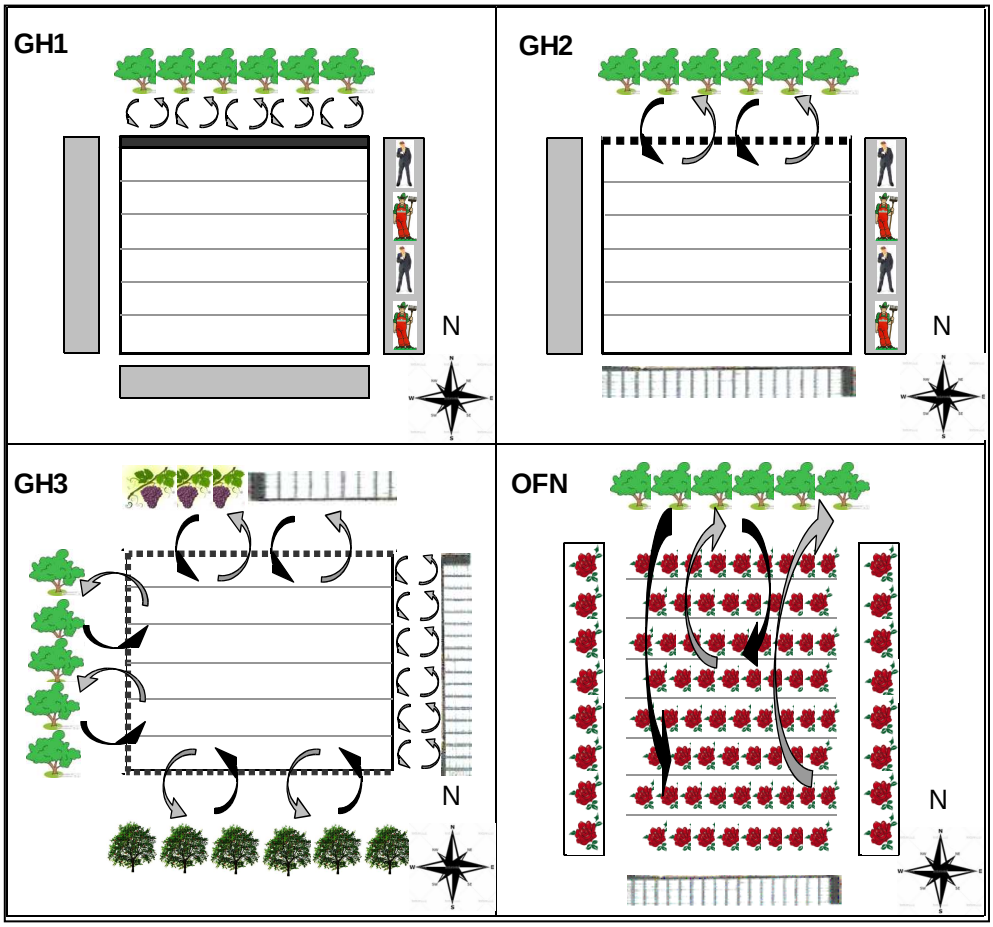

Figure 1 – Picture referring to four different cultivation scenarios considered in this study. a) house completely closed (GH1); b) house with a northern lateral opening (GH2); c) house with three lateral openings (north, west, south) (GH3); d) open field nursery (OFN).

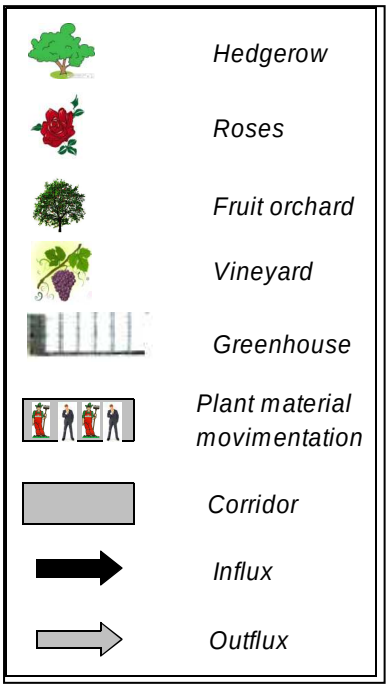

Figure 2 – Symbols used in the Figure 1 for indicating the greenhouses' surroundings.

Data analysis

Data were analysed using Spatial Analysis by Distance IndicEs (SADIE) and 'red-blue' plot methodology (Perry et *al*., 1999; Winder et *al*., 2001; Perry and Dixon, 2002) was used to visualize patches (areas of relatively high counts) and gaps (areas of zero or relatively small counts) in spatial distribution of insects. At a given location, each sampling point had an x, y field coordinate and a corresponding count c (insect captured in a trap), which represented the value of the variable being analysed. Tests of non-randomness was based on the overall index of aggregation (Ia) ($\alpha = 0.05$) (Perry *et al.*, 1999). Local clustering indices ($v_i > 1,5$ as membership to a patch; $v_j < -1,5$ as membership to a gap) were then used to generate two-dimensional contour maps showing their spatial distribution (Perry et al., 1999). We also quantified the similarity between two spatial patterns, through the degree of spatial association between them (Perry & Dixon, 2002). The measure of spatial association was determined by the overall index of association, "X", with a positive association if $X > 0$ ($P < 0.025$) indicating the overlapping of patches or gaps between two spatial pattern; and a negative association if $X < 0$ ($P > 0.975$) indicating overlapping of patches and gaps in one spatial pattern (Perry & Dixon, 2002; Reay-Jones, 2012). The randomization method (Perry et *al*., 1999; Perry and Dixon, 2002) was used to construct a

formal test of significance in spatial association. Using this method we evaluated the similarity in the distributions of the same species observed in different sampling dates (intra-specific association) and the similarity in the distribution of two different species observed in the same sampling dates (inter-specific association). All SADIE statistics were generated with SADIESHELL version 1.5.3 (Rothamsted Experimental Station, Harpenden, Herts, UK). The software N_AShell (version 1) was used for the tests of spatial association while SURFER® (Golden Software) was used to construct bi-dimensional maps.

Table 1- Insecticides used in the different experimental sites in 2012 and 2013.

Cultivation scenario	Pyrethroids	Spinosyns	Carbamates	Avermectins	Others
GH1	X		X	X	X
GH2	X	X	X		X
GH3	X	X	X	X	X
OFN	X	X			

Results

Spatial and temporal dynamics in 2012

F. occidentalis and *T. tabaci* were the most common phytophagous thrips species in the four experimental sites and their surroundings. Among predators, those belonging to the genera *Aeolothrips* (mainly *A. intermedius* and *A. fasciatus)*, and *Orius* (mainly *O. minutus*, *O. niger, O. majusculus and O. laevigatus*) were frequently recorded. Regarding *T. tabaci*, meta-populations were totally female-biased and females of *F. occidentalis* were much more abundant than males. Therefore results regarding phytophagous thrips refer to females only. Distribution patterns are discussed for all sampling dates but figures refer to the most significant ones.

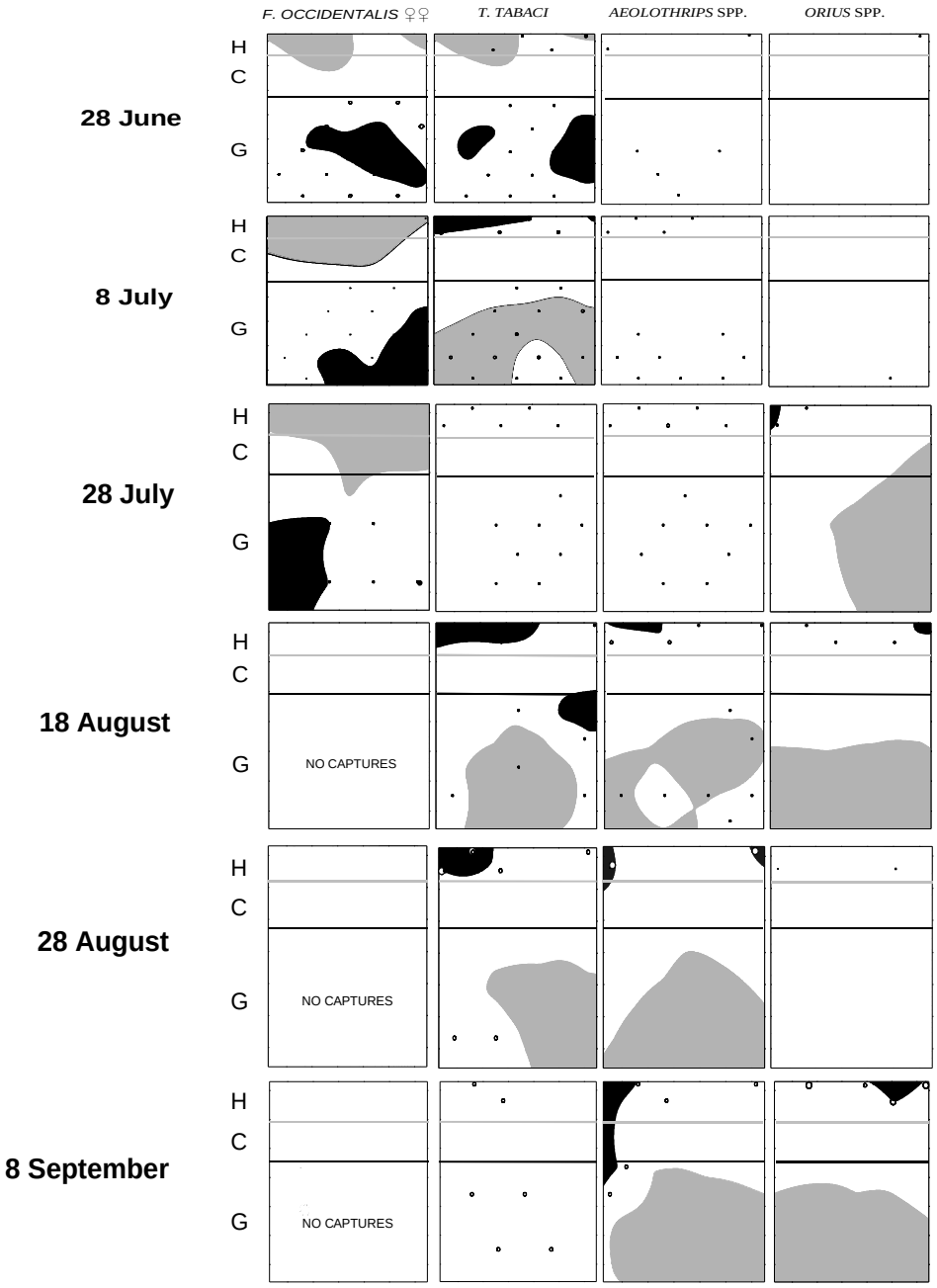

Figure 3 - Spatial patterns of *F. occidentalis*, *T. tabaci*, *Aeolothrips* spp., *Orius* spp. populations in the greenhouse GH1 on selected sampling dates during 2012. Black areas correspond to patch ($v_i > 1.5$) whilst grey correspond to gap ($v_j < -1.5$). Letters 'H', 'C', 'G' indicate 'hedgerow', 'corridor', and 'greenhouse' respectively. Points inside or outside greenhouse correspond to locations of traps with insect captures.

Table 2 - Aggregation index (I) and associated probability (p) of *F. occidentalis*, *T. tabaci*, *Aeolothrips* spp. and *Orius* spp. populations in greenhouse GH1 and its surroundings during 2012.

GH1

date	*F. occidentalis* (♀♀)		*T. tabaci*		*Aeolothrips* spp.		*Orius* spp.	
	I	P	I	P	I	P	I	P
08-Apr	0.851	0.7651	0.914	0.6361	-	-	-	-
18-Apr	0.915	0.6434	1.053	0.4704	-	-	-	-
28-Apr	0.856	0.7822	1.015	0.4121	-	-	-	-
08-May	1.148	0.2289	0.882	0.7163	1.348	0.094	-	-
18-May	1.107	0.2486	0.909	0.633	-	-	-	-
28-May	-	-	***1.723***	***0.0013***	***1.487***	***0.0155***	-	-
8-June	***1.396***	***0.0334***	1.205	0.1471	***1.61***	***0.0073***	***1.611***	***0.006***
18-June	***1.46***	***0.0187***	***1.454***	***0.023***	1.068	0.3357	-	-
28-June	***1.649***	***0.0023***	1.174	0.1684	0.862	0.7555	***1.377***	***0.0479***
8-July	***1.911***	***0.0003***	***1.817***	***0.0005***	1.32	0.0654	1.067	0.4255
18-July	***1.87***	***0.0003***	1.254	0.1178	-	-	***1.519***	***0.0163***
28-July	***1.656***	***0.0029***	1.211	0.14	1.14	0.2051	***1.583***	***0.0104***
8-Aug	0.916	0.6257	***1.769***	***0.0018***	***1.77***	***0.0016***	1.318	0.0764
18-Aug	-	-	***1.784***	***0.0005***	***1.66***	***0.0035***	***1.684***	***0.0027***
28-Aug	-	-	***1.451***	***0.0187***	***1.448***	***0.0288***	1.264	0.0828
8-Sept	-	-	-	-	***2.048***	***0.0003***	-	-
18-Sep	-	-	1.282	0.0673	-	-	-	-
28-Sep	-	-	0.991	0.4369	-	-	-	-
8-Oct	1.045	0.3199	0.804	0.9029	-	-	-	-

In April and May of 2012, *F. occidentalis* females were detected in the greenhouse GH1 (opened only at the roof). In June and July, populations were significantly aggregated and most of patches were in the centre of the greenhouse or close to contiguous greenhouses (Table 2; Figure 3). Gaps were localized in the opposite area, facing to the experimental hedgerow (Figure 3). Populations dramatically declined from August onwards probably due to plant cutting practices. A strong similarity among *F. occidentalis* distributions was found from 18 June to 18 July (Table 3).

Table 3 – Results of association test (Perry & Dixon, 2002) for of *F. occidentalis* populations in greenhouse GH1 during 2012.

F. occidentalis (♀♀)											
F. occidentalis (♀♀)	date	18-Apr *P*	28-Apr *P*	08-May *P*	18-May *P*	08-Jun *P*	18-Jun *P*	28-Jun *P*	08-Jul *P*	18-Jul *P*	28-Jul *P*	08-Aug *P*
	08-Apr	0.7445	0.1663	0.9681	0.124	0.5234	0.262	0.2958	0.6913	0.1549	0.8803	0.2951
	18-Apr		0.2899	0.0284	0.3339	***0.0146***	0.0285	***0.0195***	0.039	0.313	0.0306	0.3622
	28-Apr			0.731	0.2445	***0.0208***	0.0854	0.026	0.2991	0.4143	0.488	0.6277
	08-May				0.6351	0.2327	0.2355	0.1774	***0.0029***	0.2477	0.0502	0.1501
	18-May					0.2615	0.3265	0.4871	0.8552	0.9527	0.2254	0.3476
	08-Jun						***0.0001***	***0.0021***	0.0715	0.6206	0.0527	0.5932
	18-Jun							***0.0029***	0.0648	0.2882	0.0458	0.4187
	28-Jun								***0.0216***	0.1453	0.3334	0.2825
	08-Jul									***0.0231***	0.1201	0.0999
	18-Jul										0.898	0.4443
	28-Jul											0.0565

T. tabaci was found in the greenhouse GH1 and in the hedgerow H1 from the first sampling dates. Population densities in the greenhouse increased in early summer declining in late season. Populations showed to be aggregated in five sampling dates on the hedgerow but only twice in the greenhouse (Table 2; Figure 3). Gaps were localized along the southern side of the greenhouse. Intraspecific association was recorded only in June and August (Table 4).

Table 4 – Results of association test (Perry & Dixon, 2002) of *T. tabaci* populations in greenhouse GH1 during 2012.

T. tabaci

T. tabaci date	18-Apr P	28-Apr P	08-May P	18-May P	28-May P	08-Jun P	18-Jun P	28-Jun P	08-Jul P	18-Jul P	28-Jul P	08-Aug P	18-Aug P	28-Aug P	10-Sep P
08-Apr	0.1395	0.785	0.3062	0.4127	0.9976	0.1008	0.0527	0.3075	0.9331	0.2177	0.6931	0.9964	0.9982	0.9727	0.5526
18-Apr		0.998	0.3455	0.1183	0.9995	0.0998	0.0521	0.1643	0.978	0.4042	0.6161	0.9988	0.9301	0.9991	0.6458
28-Apr			0.8696	0.4175	***0.0112***	0.9617	0.9991	0.9865	***0.0072***	0.6734	0.4312	0.0536	0.0647	0.0387	0.2492
08-May				0.4163	0.859	0.0877	0.0867	0.1077	0.8416	0.4274	0.3691	0.6114	0.776	0.8195	0.7072
18-May					0.408	0.6322	0.5222	0.7216	0.1741	0.4914	0.1273	0.7747	0.328	0.697	0.1699
28-May						0.9338	0.9932	0.8518	***0.0006***	0.2377	0.0989	***0.0017***	***0.0003***	***0.002***	0.2689
08-Jun							***0.0032***	***0.0122***	0.9644	0.2512	0.1515	0.8435	0.9044	0.9986	0.8227
18-Jun								***0.0096***	0.9595	0.3287	0.34	0.8284	0.9895	0.9981	0.9431
28-Jun									0.8986	0.0768	0.4957	0.4799	0.6317	0.9638	0.9858
08-Jul										0.2682	0.1757	***0.0017***	***0.005***	***0.0164***	0.4531
18-Jul											0.8147	0.7692	0.3632	0.8048	-
28-Jul												-	-	-	-
08-Aug													-	-	-
18-Aug														***0.0093***	0.4168
28-Aug															0.0647
10-Sep															

Predaceous thrips were detected in the greenhouse and on the hedgerow from the first sampling date onwards (Figure 3). *Aeolothrips* spp. densities increased from late June to late August, then declined. Their distribution was aggregated from late May to early June and from August onwards when patches were observed on the hedgerow (Table 2, Figure 3). A single aggregation was noticed in the greenhouse in September whereas gaps were seen in the area opposite to the hedgerow. Positive intra-specific associations among subsequent dates were registered in spring and late summer (Table 5).

Table 5 – Results of association test (Perry & Dixon, 2002) of *Aeolothrips* spp. populations in greenhouse GH1 during 2012.

Aeolothrips spp.

Aeolothrips spp.	date	08-Jun	08-Jun	28-Jun	08-Jul	28-Jul	08-Aug	18-Aug	28-Aug	08-Sep
		P	*P*	*P*	*P*	*P*	*P*	*P*	*P*	*P*
08-May		***0.0001***	0.9998	0.5223	0.0313	0.0268	***0.0001***	***0.0034***	***0.0001***	0.0383
28-May		***0.0001***	0.9911	0.8278	0.0536	0.0965	***0.0001***	***0.0049***	***0.0002***	0.0354
08-Jun			0.9825	0.8657	***0.041***	0.1726	***0.0001***	***0.0075***	***0.0001***	0.0655
18-Jun				0.6865	0.5658	0.8136	0.9986	0.7559	0.9492	0.9144
28-Jun					0.7009	0.3577	0.7422	0.7305	0.4821	0.591
08-Jul						0.2817	0.0648	***0.0009***	0.1497	0.1101
28-Jul							-	-	-	-
08-Aug								-	-	-
18-Aug									***0.0159***	0.1593
28-Aug										***0.0242***
08-Sep										

Anthocorids belonging to the genus *Orius* were found only in correspondence of the hedgerow with significant aggregation on five sampling dates (Table 2). Gaps were localized into the greenhouse (Figure 3). *Orius* densities peaked on 18 August and 8 September and their distributions were positively associated in August (Tab. 6).

Table 6 – Results of association test (Perry & Dixon, 2002) of *Orius* spp. populations in greenhouse GH1 during 2012.

Orius spp.

Orius spp.	date	08-Jun	08-Jul	08-Jul	18-Jul	28-Jul	08-Aug	18-Aug	28-Aug	08-Sep
		P	*P*	*P*	*P*	*P*	*P*	*P*	*P*	*P*
08-Jun			***0.0001***	0.9936	***0.0001***	0.216	***0.0004***	***0.0001***	***0.0006***	0.0369
08-Jul				0.9877	***0.0092***	0.2646	***0.004***	***0.0001***	***0.009***	***0.0248***
08-Jul					0.9988	0.9991	0.9997	0.9998	0.9999	0.882
18-Jul						0.135	***0.0001***	***0.0001***	***0.0001***	-
08-Aug								***0.0001***	***0.0001***	0.0834
18-Aug									***0.0003***	0.0492
28-Aug										0.093
08-Sep										

The distributions of *F. occidentalis* and *T. tabaci* were positively associated on 28 June, when pests occurred close to the main entry of the greenhouse (Table 7). A single association between *F. occidentalis* and *Orius* spp. was detected on July 8 (Table 8) in the south-eastern side of the greenhouse whereas *F. occidentalis* and *Aeolothrips* spp. were never associated. *T. tabaci* and *Aeolothrips* spp. were frequently associated in the hedgerow (Table 9) where this pest was also associated with *Orius* spp. (Table 10). Finally, positive associations were registered between predatory thrips and predatory bugs in the hedgerow (Table 11).

Table 7 – Results of interspecific association test (Perry & Dixon, 2002) between *F. occidentalis* and *T. tabaci* populations in GH1 during 2012. Grey cells indicate association test performed on spatial patterns observed in the same date.

		T. tabaci													
	date	***08-Apr*** ***P***	**18-Apr** ***P***	**28-Apr** ***P***	**08-May** ***P***	**18-May** ***P***	**28-May** ***P***	**08-Jun** ***P***	**18-Jun** ***P***	**28-Jun** ***P***	**08-Jul** ***P***	**18-Jul** ***P***	**28-Jul** ***P***	**08-Aug** ***P***	**18-Aug** ***P***
F. occidentalis (♀♂)	**08-Apr**	0.9344	0.3132	0.7532	0.1495	0.2234	0.2984	0.0429	0.3011	0.0675	0.378	0.3024	0.0659	0.2753	0.0732
	18-Apr	0.1213	0.0508	0.9425	0.1205	0.5403	0.9009	0.0423	0.1237	0.063	0.9668	0.569	0.3706	0.8388	0.8351
	28-Apr	0.16	0.2268	0.795	0.0313	0.3261	0.8707	***0.005***	0.0854	0.323	0.5129	0.2309	0.1782	0.8158	0.9402
	08-May	0.0756	**0.0195**	0.9127	0.4924	0.5276	0.9929	0.5238	0.41	0.419	0.9961	0.3127	0.8637	0.9991	0.8683
	18-May	0.5324	0.9699	0.6087	0.0303	0.9111	0.5759	0.1607	0.3847	0.0911	0.873	0.4638	0.5148	0.3508	0.3531
	08-Jun	0.0285	0.0888	0.9771	0.0909	0.7282	0.9764	***0.0002***	***0.0012***	0.0464	0.9844	0.2441	0.4712	0.8944	0.9953
	18-Jun	0.0438	0.0302	0.9994	0.0721	0.5362	0.9784	***0.0003***	***0.0002***	***0.0039***	**0.9901**	0.0941	0.3981	0.8982	0.981
	28-Jun	0.3311	***0.0174***	0.9942	0.1838	0.8463	0.9502	***0.0003***	***0.0116***	***0.0199***	0.9486	0.3054	0.3014	0.8623	0.9312
	08-Jul	0.0447	***0.0001***	0.9885	0.3598	0.314	0.9999	0.1306	0.0617	0.387	0.9919	0.7884	0.548	0.9993	0.9947
	18-Jul	0.6554	***0.0001***	0.917	0.5577	0.0266	0.8366	0.3689	0.3181	0.3429	0.2279	***0.0189***	0.3404	0.878	0.2781
	28-Jul	***0.0043***	0.1737	0.9596	0.2038	0.5957	0.9939	0.1762	0.0788	0.1462	0.9997	0.4621	0.5807	0.9924	0.9788
	08-Aug	0.2746	0.1253	0.8976	0.5538	0.6394	0.9861	0.2446	0.3963	0.3047	0.9992	0.8305	0.7464	0.9757	0.6893

Table 8 – Results of interspecific association test (Perry & Dixon, 2002) between *F. occidentalis* and *Orius* spp. populations in GH1 during 2012. Grey cells indicate association test performed on spatial patterns observed in the same date.

Orius spp.

F. occidentalis (♀+♂) date	08-Jun *P*	28-Jun *P*	08-Jul *P*	18-Jul *P*	28-Jul *P*	08-Aug *P*	18-Aug *P*	28-Aug *P*	08-Sep *P*
08-Apr	0.1013	0.0621	0.6922	***0.0292***	0.859	0.1401	0.1905	0.1478	0.0314
18-Apr	0.938	0.9838	0.1295	0.2944	0.881	0.936	0.9568	0.9468	-
28-Apr	0.7476	0.8281	0.2193	0.3454	0.9834	0.8532	0.8012	0.8292	0.713
08-May	0.9952	0.999	***0.005***	0.7986	0.9232	0.9905	0.9989	0.9959	-
18-May	0.3915	0.6313	0.9549	***0.0001***	0.3401	0.4808	0.4683	0.4783	0.7901
08-Jun	0.9428	0.9967	0.1995	0.4051	0.9825	0.9869	0.971	0.9743	0.8287
18-Jun	0.9128	0.9881	0.1524	0.4101	0.9933	0.9601	0.9712	0.9545	-
28-Jun	0.7958	0.8261	0.0558	0.2442	0.9983	0.9079	0.9104	0.8819	0.7655
08-Jul	0.9969	0.9982	***0.0001***	0.9957	0.9961	0.9999	0.9998	0.9999	-
18-Jul	0.47	***0.0448***	***0.0048***	0.999	0.9987	0.5244	0.738	0.5498	-
28-Jul	0.9988	0.9997	0.2295	0.4564	0.7143	0.9982	0.9972	0.9993	-
08-Aug	0.8431	0.7898	0.1655	0.2776	0.8299	0.9069	0.9688	0.9221	-

Table 9 - Results of interspecific association test (Perry & Dixon, 2002) between *T. tabaci* and *Aeolothrips* spp. and *T. tabaci* populations in GH1 during 2012. Grey cells indicate association test performed on spatial patterns observed in the same date.

Aeolothrips spp..

T. tabaci date	08-May *P*	28-May *P*	08-Jun *P*	18-Jun *P*	28-Jun *P*	08-Jul *P*	28-Jul *P*	08-Aug *P*	18-Aug *P*	28-Aug *P*	08-Sep *P*
08-Apr	0.9616	0.9963	0.9983	0.127	0.0635	0.9036	0.2393	0.9986	0.9589	0.9938	0.8892
18-Apr	0.9999	0.9972	0.9989	0.0004	0.4783	0.3207	0.9615	0.9987	0.7973	0.9848	0.8927
28-Apr	0.0325	***0.0211***	***0.0219***	0.9399	0.9175	0.1948	0.1502	0.0336	***0.0149***	0.0879	0.4104
08-May	0.8539	0.8588	0.8142	0.28	0.7201	0.9102	0.5265	0.8251	0.9218	0.8417	0.6909
18-May	0.7028	0.4844	0.5959	0.0544	0.9108	0.0351	0.6075	0.6373	0.2766	0.7544	0.4384
28-May	***0.0001***	***0.0001***	***0.0001***	0.9963	0.884	0.0265	0.057	***0.0001***	***0.0019***	***0.0006***	0.0396
08-Jun	0.9916	0.922	0.9317	0.0417	0.6233	0.9868	0.6288	0.9478	0.9767	0.9159	0.8244
18-Jun	0.9986	0.9922	0.9929	0.0894	0.1405	0.9731	0.6136	0.9842	0.9942	0.9399	0.7834
28-Jun	0.9504	0.7653	0.7627	0.276	0.2847	0.9698	0.7421	0.7597	0.9252	0.5109	0.6885
08-Jul	***0.0013***	***0.0025***	***0.0004***	0.8388	0.8326	***0.0148***	0.1057	***0.0013***	***0.0003***	***0.0017***	***0.0171***
18-Jul	0.4693	0.2536	0.2045	0.472	0.5439	0.7435	0.3442	0.2066	0.4852	0.2461	-
28-Jul	0.262	0.1261	0.2907	0.3126	0.692	0.227	0.1159	0.1919	0.1854	0.3318	0.68
08-Aug	**0.0029**	**0.0027**	**0.0004**	0.9887	0.688	**0.2496**	0.2729	***0.0009***	0.0445	***0.0002***	0.157
18-Aug	***0.0017***	***0.0001***	***0.0001***	0.8505	0.9386	0.0783	0.542	***0.0005***	***0.0102***	***0.0001***	0.0258
28-Aug	***0.0003***	***0.0025***	***0.0076***	0.9863	0.2622	0.0702	0.1113	***0.0001***	***0.0123***	***0.0047***	0.1428
08-Sep	0.3942	0.3332	0.4863	0.622	0.5391	0.1296	0.1425	0.317	0.0484	0.6701	0.1881

Table 10 - Results of interspecific association test (Perry & Dixon, 2002) between *T. Tabaci* and *Orius* spp. populations in GH1 during 2012. Grey cells indicate association test performed on spatial patterns observed in the same date.

Orius spp.

T. tabaci date	08-Jun *P*	28-Jun *P*	08-Jul *P*	18-Jul *P*	28-Jul *P*	08-Aug *P*	18-Aug *P*	28-Aug *P*	08-Sep *P*
08-Apr	0.9983	0.9999	0.0627	0.9273	0.7535	0.9986	0.9997	0.9987	0.9806
18-Apr	0.9261	0.8236	***0.009***	0.9143	0.9999	0.9875	0.9951	0.9898	0.7466
28-Apr	0.0543	0.1254	0.952	0.4648	***0.0212***	0.0423	0.0155	0.0533	0.2374
08-May	0.6	0.8273	0.5084	0.0647	0.857	0.6813	0.6573	0.7051	0.586
18-May	0.6866	0.4457	0.2614	0.9654	0.8507	0.6969	0.6266	0.7318	0.4217
28-May	0.0249	***0.0214***	0.9999	***0.0001***	***0.0029***	***0.0001***	***0.0003***	***0.0003***	0.1917
08-Jun	0.7873	0.908	0.3355	0.061	0.989	0.9063	0.8802	0.8975	0.8294
18-Jun	0.8359	0.8886	0.1311	0.7677	0.9949	0.9803	0.9453	0.9704	0.7243
28-Jun	0.3197	0.3361	0.398	0.0292	0.9403	0.5841	0.6075	0.6228	0.555
08-Jul	***0.0191***	***0.0019***	0.9446	0.6716	0.0645	***0.005***	***0.0009***	***0.0071***	0.071
18-Jul	0.1867	0.2458	0.4268	0.9847	0.6653	0.1285	0.315	0.1816	-
28-Jul	0.5528	0.4959	0.7283	0.4909	0.51	0.2586	0.3079	0.274	0.9716
08-Aug	***0.0002***	***0.0007***	0.9999	***0.0151***	***0.0245***	***0.0001***	***0.0001***	***0.0001***	0.0795
18-Aug	***0.0126***	***0.0012***	0.9892	***0.0036***	0.0415	***0.0011***	***0.0017***	***0.0029***	0.0864
28-Aug	0.0948	0.0431	0.9984	0.2257	***0.0001***	***0.0215***	***0.0071***	***0.0223***	0.4403
08-Sep	0.7697	0.6814	0.4797	-	0.1556	0.6581	0.4693	0.6506	0.3527

Table 11 - Results of interspecific association test (Perry & Dixon, 2002) between *Aeolothrips* spp. and *Orius* spp. populations in GH1 during 2012. Grey cells indicate association test performed on spatial patterns observed in the same date.

Orius spp.

Aeolothrips spp. date	08-Jun *P*	28-Jun *P*	08-Jul *P*	18-Jul *P*	28-Jul *P*	08-Aug *P*	18-Aug *P*	28-Aug *P*	08-Sep *P*
08-May	0.0788	0.0906	0.9999	0.0045	***0.0001***	***0.0014***	***0.0071***	***0.0012***	0.3746
28-May	***0.0149***	***0.0238***	0.9999	***0.0001***	***0.0031***	***0.0001***	***0.0004***	***0.0002***	0.2735
08-Jun	***0.0095***	***0.0094***	0.9998	***0.0001***	***0.0016***	***0.0001***	***0.0003***	***0.0002***	0.0945
18-Jun	0.8469	0.69	0.0334	0.8293	0.9999	0.9551	0.9573	0.9668	0.7554
28-Jun	0.7584	0.7225	0.3185	0.8429	0.1414	0.7387	0.8233	0.7373	0.7422
08-Jul	0.4278	0.2012	0.3983	0.9807	0.1367	0.1401	0.1782	0.1548	0.3006
28-Jul	0.7342	0.8419	0.8456	0.7126	***0.0135***	0.2883	0.26	0.2934	0.843
08-Aug	***0.0086***	***0.0059***	0.9999	***0.0001***	***0.0024***	***0.0002***	**0.0001**	**0.0003**	0.1482
18-Aug	0.09	***0.0151***	0.7558	0.7572	0.0255	***0.0186***	***0.0165***	**0.0192**	0.3981
28-Aug	***0.0018***	***0.0001***	0.9992	**0.0001**	***0.0079***	***0.0001***	***0.0001***	***0.0001***	0.1103
08-Sep	0.2066	0.1288	0.93	-	0.1637	0.0943	0.0549	0.0914	***0.0001***

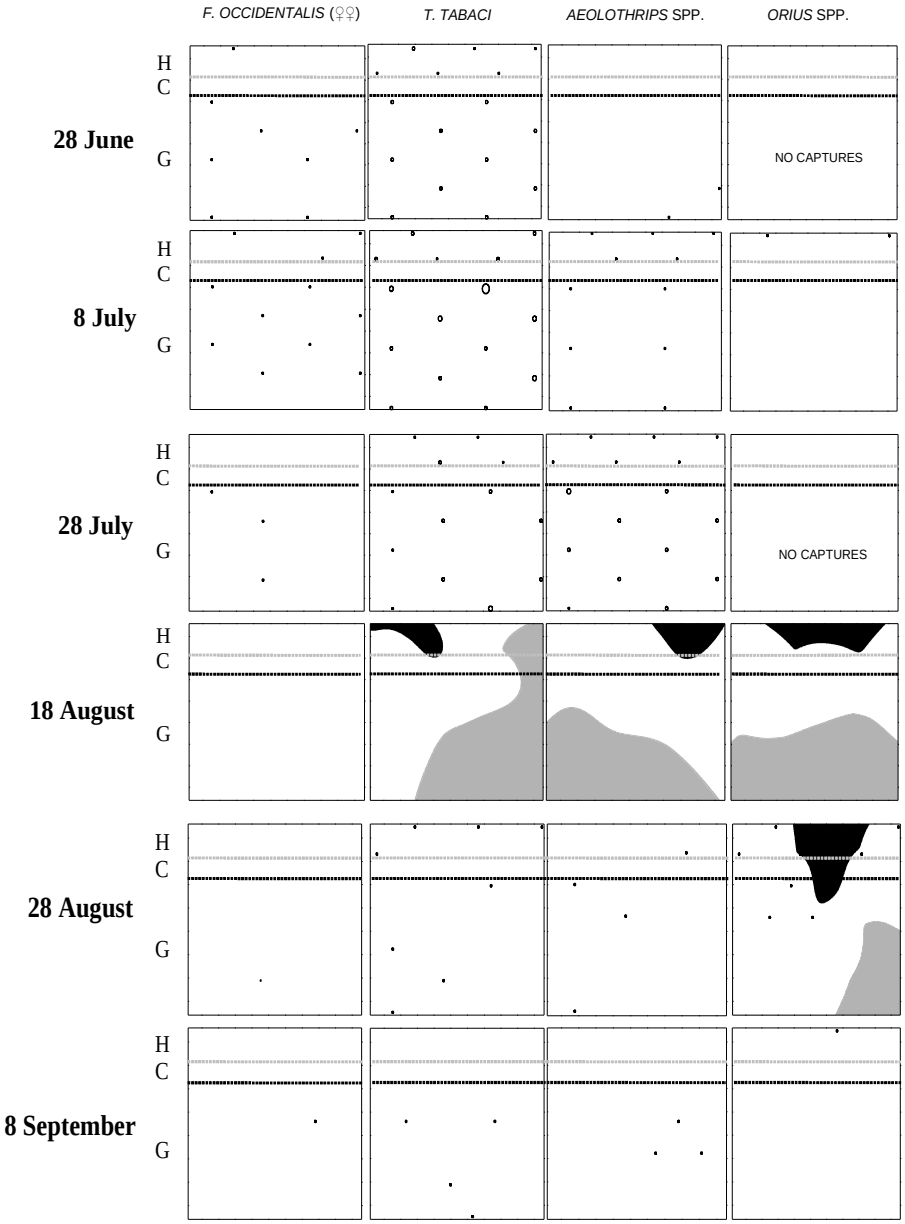

Figure 4 - Spatial patterns of *F. occidentalis*, *T. tabaci*, *Aeolothrips* spp., *Orius* spp. populations in the greenhouse GH2 on selected sampling dates during 2012. Black areas correspond to patch ($v_i > 1.5$) whilst grey correspond to gap ($v_j < -1.5$). Letters 'H', 'C', 'G' indicate 'hedgerow', 'corridor', and 'greenhouse' respectively. Points inside or outside greenhouse correspond to locations of traps with insect captures.

Table 12 - Aggregation index (I) and associated probability (p) of *F. occidentalis*, *T. tabaci*, *Aeolothrips* spp. and *Orius* spp. populations in greenhouse GH2 and its surroundings during 2012.

GH2

date	*F. occidentalis* (♀♀)		*T. tabaci*		*Aeolothrips* spp.		*Orius* spp.	
	I	P	I	P	I	P	I	P
08-apr	-	-	1.0670	0.3002	-	-	-	-
18-apr	-	-	1.1990	0.1263	-	-	-	-
28-apr	0.997	0.4724	0.7500	0.9997	0.805	0.9311	-	-
08-mag	-	-	0.847	0.8229	1.295	0.0553	-	-
18-May	-	-	0.843	0.8304	-	-	-	-
28-May	-	-	0.913	0.6587	-	-	0.885	0.7503
8-June	0.997	0.4421	1,222	0.0974	1,163	0.2468	-	-
18-June	0.972	0.4995	0.725	0.9813	-	-	-	-
28-June	0.773	0.92	1.208	0.1059	1,194	0.129	-	-
8-July	0.808	0.9252	0.767	0.9193	0.993	0.4575	1.031	0.3611
18-July	0.83	0.8664	0.979	0.4828	1.102	0.2359	***1.609***	***0.0005***
28-July	0.983	0.4736	1.263	0.0841	0.993	0.4474	-	-
8-Aug	-	-	***1.336***	***0.0386***	0.847	0.8361	-	-
18-Aug	1,251	0.0684	***1.393***	***0.019***	***1.429***	***0.0126***	***1.482***	***0.0085***
28-Aug	0.76	0.9997	1,087	0.2516	0.925	0.64	***1.451***	***0.0147***
8-Sept	0.811	0.8515	0.909	0.6691	-	-	1.049	0.3876
18-Sep	-	-	-	-	-	-	-	-
28-Sep	-	-	-	-	-	-	-	-
8-Oct	-	-	-	-	-	-	-	-

F. occidentalis was observed inside the greenhouse GH2 from April onwards, and occasionally in the contiguous hedgerow (Figure 4). The highest population densities were noticed in June and the lowest in mid-summer. *F. occidentalis* population was never (Table 12; Figure 4) and no associations were observed among *F. occidentalis* populations over the time.

The presence of *T. tabaci* was homogeneous in the greenhouse in the first part of the season with highest densities in July. This pest was also detected in the contiguous hedgerow during most of dates (Figure 4). Populations were aggregated in August both inside greenhouse and in thehedgerow (Table 12; Figure 4). No intraspecific association patterns were found over the time.

Predaceous thrips (*Aeolothrips* spp.) were recorded frequently in the greenhouse and

outside and their densities reached the highest levels between July and August. They were found to be aggregated in the hedgerow on 18 August (Table 12; Figure 4). No similarities between population distributions were evidenced.

Table 13 – Results of association test (Perry & Dixon, 2002) of *Orius* spp. populations in greenhouse GH2 during 2012.

		Orius spp.			
	date	**18-Jul**	**18-Aug**	**28-Aug**	**08-Sep**
		P	*P*	*P*	*P*
Orius spp.	**28-May**	0.4323	0.0307	0.0747	***0.0215***
	08-Jul	0.3066	0.28	0.2847	0.43
	18-Jul		0.3225	0.2553	0.2597
	18-Aug			***0.0001***	***0.0001***
	28-Aug				***0.0001***

Anthocorids were found especially in mid-summer where they were aggregated in the hedgerow and the greenhouse on 18 July and 28 August; this phenomenon was also observed on August 18 but only in the hedgerow (Table 12; Figure 4). Gaps involved the internal side of the greenhouse, opposite to the hedgerow (Figure 4). Intraspecific associations were noticed in late summer (Table 13).

Table 14 - Associations between *T. tabaci* and *Aeolothrips* spp. populations in greenhouse GH2 during 2012.

		Aeolothrips spp.								
	date	**28-Apr**	**08-May**	**08-Jun**	**28-Jun**	**08-Jul**	**18-Jul**	**28-Jul**	**08-Aug**	**28-Aug**
		P	*P*	*P*	*P*	*P*	*P*	*P*	*P*	*P*
T. tabaci	**08-Apr**	0.2499	0.4999	0.6285	0.0911	0.9281	0.1892	0.055	0.2457	0.3571
	18-Apr	0.5417	0.2598	0.8654	0.1623	0.8658	0.1729	0.0688	0.4217	0.5111
	28-Apr	0.3249	0.5362	0.239	0.871	0.157	0.3317	0.5347	0.502	0.2387
	08-May	0.5463	0.5379	0.7319	0.1454	0.9105	0.1786	0.0541	0.316	0.2138
	18-May	0.4292	0.1138	0.2629	0.5801	0.7626	0.0697	0.2293	0.1867	0.0395
	28-May	0.4587	0.0343	0.7673	0.2034	0.7299	0.226	0.1334	0.489	0.2198
	08-Jun	0.8572	0.5696	0.754	***0.0354***	0.8695	0.4754	***0.0313***	0.5315	0.6796
	18-Jun	0.155	0.4791	0.0693	0.9359	0.4805	0.1426	0.5109	0.3453	0.0603
	28-Jun	0.7355	0.1667	0.7721	0.0416	0.7015	0.2642	0.0558	0.6382	0.6684
	08-Jul	0.174	0.7722	0.712	0.3332	0.9032	0.1285	0.1534	0.2162	0.2602
	18-Jul	0.3271	0.328	0.7346	0.6123	0.8311	0.1255	0.2466	0.1039	0.1413
	28-Jul	0.588	0.7763	0.8753	0.0353	0.965	0.3869	0.0384	0.5672	0.8242
	08-Aug	0.6069	0.0265	0.5034	0.2007	0.6287	0.0311	0.0528	0.1105	0.1897
	18-Aug	0.7002	0.3847	***0.0119***	0.9909	0.1361	0.4416	0.9193	0.8932	0.4829
	28-Aug	0.4438	0.9571	0.4624	0.8687	0.1923	0.9029	0.8707	0.7113	0.7115
	08-Sep	0.9406	***0.0061***	***0.0263***	0.6252	0.4218	0.5282	0.5828	0.8775	0.6638
	28-Sep	0.1368	0.9079	0.734	0.4247	0.59	0.4567	0.4302	**0.0252**	0.2455
	08-Oct	0.9358	***0.0033***	***0.0231***	0.5887	0.5626	0.3293	0.4171	0.8957	0.6061

There were no positive associations between females *F. occidentalis* and *T. tabaci*, as well as *F. occidentalis* and beneficial arthropods. However, *T. tabaci* was found to be positively associated with predatory thrips at the end of June and at the end of July (Table 14).

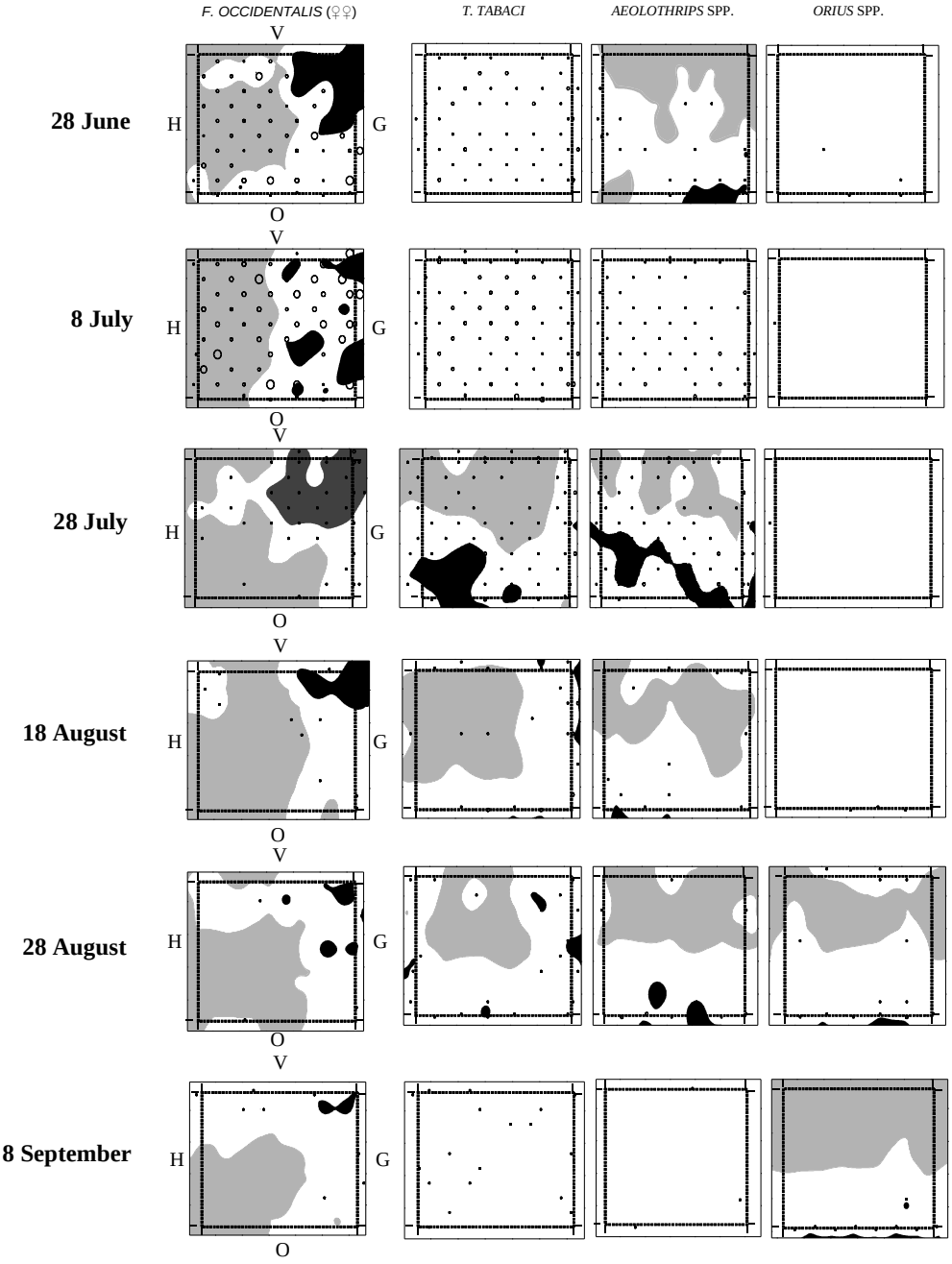

Figure 5 - Spatial patterns of *F. occidentalis*, *T. tabaci*, *Aeolothrips* spp., *Orius* spp. populations in the greenhouse GH3 on selected sampling dates during 2012. Black areas correspond to patch ($v_i > 1.5$) whilst grey correspond to gap ($v_j < - 1.5$). Letters 'H', 'C', 'G' indicate 'hedgerow', 'corridor', and 'greenhouse' respectively. Points inside or outside greenhouse correspond to locations of traps with insect captures.

F. occidentalis was detected inside greenhouse from spring onwards and population densities peaked in summer. A significant spatial structure was observed in most of dates. Populations were aggregated in correspondence of the main entry to the greenhouse (on the north-eastern corner) whereas gaps were found in the opposite side facing to the hedgerow and outdoor crops (Table 15; Figure 5). Aggregations were also seen in correspondence of the contiguous greenhouses from June onwards. Strong similarities in population distribution were found among subsequent sampling dates (Table 16).

Table 15 - Aggregation index (I) and associated probability (p) of *F. occidentalis*, *T. tabaci*, *Aeolothrips* spp. and *Orius* spp. populations in greenhouse GH3 and its surroundings during 2012 .

GH3

date	*F. occidentalis* (♀♀)		*T. tabaci*		*Aeolothrips* spp.		*Orius* spp.	
	I	**P**	**I**	**P**	**I**	**P**	**I**	**P**
08-apr	1.2350	0.1044	0.866	0.7726	-	-	-	-
18-apr	0.903	0.6755	1.1720	0.1554	-	-	-	-
28-apr	***1.4190***	***0.0308***	***1.3350***	***0.0466***	1.1000	0.2349	-	-
08-mag	1.1060	0.2604	1.0240	0.3811	1.1730	0.1685	-	-
18-May	0.979	0.4975	***1.3260***	***0.0474***	-	-	-	-
28-May	***1.5240***	***0.0115***	0.965	0.5037	-	-	-	-
8-June	***1.4560***	***0.0197***	1.1520	0.172	0.972	0.504	-	-
18-June	***2.2770***	***0.0003***	1.3050	0.0617	1.1020	0.2284	-	-
28-June	***2.1340***	***0.0003***	1.1690	0.1513	***1.5680***	***0.0083***	1.2050	0.1215
8-July	***1.7840***	***0.0011***	1.3430	0.0515	1.0290	0.3592	1.0110	0.4637
18-July	***1.9360***	***0.0003***	***1.6920***	***0.0031***	***1.3990***	***0.0285***	1.2000	0.1251
28-July	***2.7550***	***0.0003***	***1.7300***	***0.0013***	***1.4600***	***0.023***	1.1730	0.1498
8-Aug	***1.9480***	***0.0003***	1.3380	0.0518	1.1670	0.1608	-	-
18-Aug	***2.0970***	***0.0003***	***1.6480***	***0.0048***	***1.4220***	***0.0243***	1.3120	0.0569
28-Aug	***1.7030***	***0.0013***	***1.3370***	***0.0441***	***1.4620***	***0.0171***	***1.4630***	***0.0219***
8-Sept	***1.5700***	***0.0061***	0.814	0.9079	0.841	0.8499	***1.8650***	***0.0003***
18-Sep	1.6400	0.0041	0.923	0.6224	-	-	1.1970	0.1432
28-Sep	2.2160	0.0003	1.1180	0.209	-	-	1.1390	0.1924
8-Oct	2.0190	0.0003	1.1800	0.1393	-	-	-	-

Table 16 - Results of association test (Perry & Dixon, 2002) of *F. occidentalis* populations in greenhouse GH3 during 2012 .

F. occidentalis (♀♀)																		
F. occidentalis (♀♀)	date	18-Apr	28-Apr	08-May	18-May	28-May	08-Jun	18-Jun	28-Jun	08-Jul	18-Jul	28-Jul	08-Aug	18-Aug	28-Aug	08-Sep	18-Sep	28-Sep	10-Oct
		P	*P*	*P*	*P*	*P*	*P*	*P*	*P*	*P*	*P*	*P*	*P*	*P*	*P*	*P*	*P*	*P*	*P*
	08-Apr	***0.0001***	***0.0011***	0.3236	0.9379	0.6063	0.2297	0.9999	0.9984	0.9901	0.9924	0.5095	0.9973	0.9078	0.9676	0.7848	0.6083	0.522	0.8266
	18-Apr		***0.0001***	***0.0001***	0.4651	0.5054	0.7573	0.9897	0.1087	0.3983	0.4762	0.1383	0.872	0.0447	0.3395	0.5367	0.5591	0.1412	0.378
	28-Apr			***0.0042***	0.3472	0.0796	0.2528	0.4155	***0.0006***	0.0016	0.1308	***0.0004***	0.0413	***0.0001***	***0.0021***	0.482	0.4817	0.2615	0.5502
	08-May				0.0645	0.1894	0.9961	0.8582	0.0592	0.1071	0.6847	0.3778	0.9352	0.7542	0.7244	0.8334	0.5548	0.3624	0.6016
	18-May					***0.0066***	0.4441	0.097	0.1282	0.1715	0.0402	0.2802	0.5176	0.555	0.8109	0.8498	0.3625	0.617	0.6229
	28-May						***0.0005***	***0.0008***	***0.0068***	0.1255	0.0964	***0.018***	0.2282	0.2785	0.1957	0.381	***0.0245***	0.054	0.1938
	08-Jun							***0.013***	0.1086	0.2696	0.1521	***0.0001***	***0.0138***	***0.0207***	0.0188	0.2548	0.2101	0.0526	0.0952
	18-Jun								***0.0001***	***0.0001***	***0.0001***	***0.0001***	***0.0001***	***0.0001***	***0.0001***	0.1032	0.2049	0.0484	***0.0053***
	28-Jun									***0.0001***	***0.0001***	***0.0001***	***0.0001***	***0.0001***	***0.0001***	0.1429	0.1534	0.067	***0.0087***
	08-Jul										***0.0001***	***0.0001***	***0.0001***	***0.0001***	***0.0001***	0.3261	0.2259	0.118	0.0698
	18-Jul											***0.0002***	***0.0001***	***0.0001***	***0.0001***	0.1466	0.1517	***0.0065***	***0.0157***
	28-Jul												***0.0001***	***0.0001***	***0.0001***	0.1173	0.2598	0.0527	***0.0011***
	08-Aug													***0.0001***	***0.0001***	0.0488	0.3768	0.0327	***0.0006***
	18-Aug														***0.0001***	0.0339	0.2164	***0.0098***	***0.0059***
	28-Aug															***0.0249***	0.063	***0.0037***	***0.0025***
	08-Sep																***0.0001***	***0.0001***	***0.0001***
	18-Sep																	***0.0001***	***0.0001***
	28-Sep																		***0.0001***

T. tabaci was observed frequently inside greenhouse and its surroundings; the highest population densities were reached between May and July. Populations were aggregated in various dates and areas inside and outside greenhouses (Table 15; Figure 5). Significant similarities in the population distribution patterns over time were noticed in May and from late July to late August (Table 17).

Table 17 - Results of association test (Perry & Dixon, 2002) of *T. tabaci* populations in greenhouse GH3 during 2012.

T. tabaci

T. tabaci date	18-Apr P	28-Apr P	08-May P	18-May P	28-May P	08-Jun P	18-Jun P	28-Jun P	08-Jul P	18-Jul P	28-Jul P	08-Aug P	18-Aug P	28-Aug P	08-Sep P
08-Apr	***0.0032***	0.8124	0.2382	0.896	0.2913	0.3186	0.6452	0.9994	0.9679	0.5019	0.5729	0.5443	0.5383	0.4016	0.4583
01-Apr		0.8379	0.6809	0.9987	0.1562	0.4847	0.9362	0.9848	0.9503	0.9733	0.8144	0.781	0.6057	0.3697	0.1576
28-Apr			0.8667	0.7676	0.9829	0.9944	0.9977	0.7146	0.5277	0.1107	***0.0069***	***0.0223***	***0.0084***	***0.0044***	0.0312
08-May				***0.0242***	0.4397	0.147	0.2456	0.776	0.2026	0.499	0.8307	0.8792	0.5767	0.8471	0.7797
18-May					***0.0102***	0.9091	***0.0024***	0.7878	0.3369	0.3724	0.9333	0.9596	0.9166	0.9203	0.4272
28-May						0.517	***0.0001***	0.9005	0.5367	0.9717	0.997	0.9798	0.938	0.9574	0.6841
08-Jun							0.1411	0.0264	0.1209	0.24	0.8888	0.9407	0.9997	0.9879	0.8765
18-Jun								0.0413	0.1023	0.9952	0.9833	0.9983	0.9902	0.979	0.4808
28-Jun									0.1299	0.9214	0.6058	0.3663	0.6658	0.8413	0.6091
08-Jul										-	-	-	-	-	-
18-Jul											***0.0001***	0.0344	0.6869	0.3778	0.951
28-Jul												***0.0001***	***0.0089***	***0.0172***	0.7261
08-Aug													***0.0001***	***0.0006***	0.4681
18-Aug														***0.0001***	0.1454
28-Aug															0.3583
08-Sep															

Predaceous thrips were found both inside greenhouse and its surroundings. Predatory thrips population reached the highest density in late July. Populations were aggregated in June, July and August with patches localized in the fruit orchard and the contiguous areas of the greenhouse (Table 15; Figure 5). Similarities in population structures over time were observed in several sampling dates (Table 18).

Table 18 - Results of association test (Perry & Dixon, 2002) of *Aeolothrips* spp. populations in greenhouse GH3 during 2012

Aeolothrips spp.

Aeolothrips spp.	date	08-May	08-Jun	18-Jun	28-Jun	08-Jul	18-Jul	28-Jul	08-Aug	18-Aug	28-Aug	08-Sep
		P	*P*	*P*	*P*	*P*	*P*	*P*	*P*	*P*	*P*	*P*
	28-Apr	0.9996	0.8524	0.9999	0.8148	0.9886	0.9942	0.077	0.2511	0.0011	0.0081	0.4194
	08-May		***0.0001***	***0.0004***	0.6947	0.3746	0.9201	0.8964	0.9742	0.9852	0.8727	0.9431
	08-Jun			***0.0001***	0.0508	0.3375	0.893	0.1289	0.2338	0.1944	***0.0249***	0.8485
	18-Jun				***0.0002***	0.0295	0.1477	***0.024***	0.0307	0.8997	0.0548	0.7584
	28-Jun					***0.0099***	***0.0024***	***0.0001***	0.0515	0.1619	***0.0001***	0.6271
	08-Jul						***0.0058***	0.2249	0.2212	0.9117	0.8689	0.5677
	18-Jul							0.3954	0.2416	0.5563	0.3581	0.3071
	28-Jul								***0.0014***	***0.002***	***0.0015***	0.5978
	08-Aug									***0.0127***	0.0164	0.0712
	18-Aug										***0.0026***	0.1908
	28-Aug											0.393
	08-Sep											

Anthocorids showed to colonize almost exclusively the greenhouse's surroundings, especially the fruit orchard (Figure 4). Aggregation patterns were seen in August and September when the highest population density levels were reached (Table 15; Figure 5). Strong similarities in the population distribution were observed over the time (Table 19) and individuals originated mainly from the fruit orchard (Figure 5).

Table 19 - Results of association test (Perry & Dixon, 2002) of *Orius* spp. populations in greenhouse GH3 during 2012.

Orius spp.

Orius spp.	date	08-Jul	18-Jul	28-Jul	18-Aug	28-Aug	08-Sep	18-Sep	28-Sep
		P	*P*	*P*	*P*	*P*	*P*	*P*	*P*
	28-Jun	***0.0001***	***0.0001***	0.176	***0.0001***	***0.0001***	***0.0005***	***0.0001***	***0.0001***
	08-Jul		***0.0001***	0.2264	***0.0001***	***0.0001***	***0.0002***	***0.0001***	***0.0001***
	18-Jul			***0.0249***	***0.0001***	***0.0001***	***0.0044***	***0.0058***	0.0323
	28-Jul				0.9591	0.7063	0.5407	0.6105	0.7334
	18-Aug					***0.0001***	***0.0001***	***0.0001***	***0.0001***
	28-Aug						***0.0071***	***0.0037***	***0.0058***
	08-Sep							***0.0001***	***0.0001***
	18-Sep								***0.0001***
	28-Sep								

F. *occidentalis* was found to be positively associated with *T. tabaci* at the beginning of July and October (Table 20). Unlike, no associations between *F. occidentalis* and beneficial arthropods were found. In contrast, *T. tabaci* was observed to be positively associated with *Aeolothrips* spp. and with *Orius* spp. inside and outside greenhouse (Tables 21, 22). Both natural antagonists were found to be associated on various sampling dates inside but especially outside the greenhouse, in the orchard area (Table 23).

Table 20 - Results of interspecific association test (Perry & Dixon, 2002) between *F. occidentalis* and *T. tabaci* populations in GH3 during 2012. Grey cells indicate association test performed on spatial patterns observed in the same date.

		T. tabaci																		
	date	08-Jul	18-Jul	28-Jul	08-May	18/58	28-May	08-Jun	18-Jun	28-Jun	08-Jul	18-Jul	28-Jul	08-Aug	18-Aug	28-Aug	08-Sep	18-Sep	18-Sep	08-Oct
		p	*p*	*p*	*p*	*p*	*p*	*p*	*p*	*p*	*p*	*p*	*p*	*p*	*p*	*p*	*p*	*p*	*p*	*p*
F. occidentalis (♀♀)	08-Apr	0.2016	0.5055	0.9995	0.2967	0.0277	0.0177	***0.0039***	***0.0016***	0.4118	0.2967	0.957	0.995	0.9999	0.9999	0.9999	0.6643	0.8699	0.3349	0.922
	18-Apr	***0.0001***	***0.0005***	0.9932	0.8605	0.2118	***0.0036***	0.1007	0.0469	0.5477	0.9466	0.979	0.805	0.971	0.9892	0.9236	0.4586	0.7466	0.0654	0.5889
	28-Apr	0.0732	***0.0232***	0.9812	0.9802	0.038	0.0308	0.5873	***0.0158***	0.297	0.9776	0.9998	0.9987	0.9993	0.9677	0.8935	0.241	0.966	0.3317	0.6127
	08-May	0.0722	***0.0059***	0.413	0.995	0.9662	0.6107	0.1655	0.7983	0.2626	0.885	0.7486	0.0515	0.3957	0.5135	0.3667	0.4708	0.789	0.1941	0.3739
	18-May	0.5106	0.8079	0.0253	0.9997	0.9192	0.9893	0.912	0.9518	0.286	0.6587	0.049	***0.0019***	0.0552	0.1472	0.048	0.71	0.3805	0.3316	0.0552
	28-May	0.9351	0.9988	0.0513	0.7061	0.0422	0.8485	0.9689	0.8389	0.0362	0.7007	0.0882	***0.0239***	0.2064	0.2682	0.3207	0.5675	0.491	0.0658	0.1782
	08-Jun	0.9912	0.9998	0.314	0.3511	***0.0001***	0.1795	0.9024	0.2519	0.4042	0.2474	0.1161	0.8163	0.7881	0.8389	0.8095	0.2233	0.4953	0.2514	0.158
	18-Jun	0.8211	0.9821	0.0651	0.2341	***0.0189***	0.6965	0.9944	0.8257	0.1111	0.6101	0.3681	0.6076	***0.0192***	***0.0003***	0.1343	0.4899	0.3054	0.1443	0.036
	28-Jun	0.2348	0.1204	0.0968	0.8359	0.0676	0.5987	0.9953	0.7611	0.3704	0.9683	0.9561	0.8086	0.0254	0.0023	0.004	0.2469	0.235	0.1232	0.0597
	08-Jul	0.371	0.4337	0.1372	0.8773	0.2094	0.8134	0.9435	0.529	0.4407	0.7508	0.7297	0.768	0.1718	0.0373	0.0072	0.7381	0.2099	0.1294	0.3984
	18-Jul	0.1792	0.5035	0.2552	0.6318	0.1416	0.2243	0.9998	0.7988	0.7296	0.9978	0.9486	0.6468	0.0376	***0.0001***	0.0639	0.5589	0.2765	0.0445	0.1038
	28-Jul	0.777	0.8935	0.4538	0.9121	***0.0024***	0.1544	0.953	0.0566	0.0841	0.5933	0.9955	0.9993	0.7036	0.1812	0.7787	0.1815	0.3973	0.0445	0.1012
	08-Aug	0.7436	0.7203	0.1763	0.4673	***0.0136***	0.0544	0.994	0.5069	0.2003	0.7119	0.979	0.9955	0.2252	0.0406	0.3458	0.2773	0.3033	0.2241	0.1824
	18-Aug	0.4009	0.1608	0.2266	0.441	***0.0025***	0.0146	0.9836	0.3048	0.552	0.9412	0.9997	0.9994	0.5536	0.0691	0.0571	0.1291	0.4252	0.1677	0.2388
	28-Aug	0.4461	0.4325	0.4139	0.1468	0.0533	0.2072	0.9683	0.1127	0.0837	0.9048	0.9977	0.9865	0.453	***0.0033***	0.0256	0.2868	0.3865	0.1511	0.2831
	08-Sep	0.4453	0.759	0.101	0.1847	0.1548	0.365	0.709	0.1036	0.161	0.3794	0.8111	0.4297	0.237	0.0397	0.2909	0.6067	0.4112	0.7476	0.4118
	18-Sep	0.581	0.8626	0.329	0.2045	0.3874	0.8076	0.8388	0.3767	0.2144	0.7167	0.8428	0.2894	0.1868	0.048	0.2152	0.778	0.0367	0.2641	0.1061
	28-Sep	0.3696	0.8901	0.2042	0.1333	0.0864	0.3165	0.7686	***0.0085***	0.2646	0.6469	0.9073	0.1828	0.096	0.0643	0.3775	0.6156	0.0397	0.0995	***0.0108***
	08-Oct	0.4682	0.6895	0.0286	0.2406	0.1779	0.2066	0.6379	0.0573	0.2667	0.3151	0.8418	0.346	***0.0128***	***0.0246***	0.2702	0.6143	0.0703	***0.0035***	***0.0159***

Table 21 - Results of interspecific association test (Perry & Dixon, 2002) between *T. tabaci* and *Aeolothrips* spp. populations in GH3 during 2012. Grey cells indicate association test performed on spatial patterns observed in the same date.

Aeolothrips spp.

T. tabaci date	28-Apr P	08-May P	08-Jun P	18-Jun P	28-Jun P	08-Jul P	18-Jul P	28-Jul P	08-Aug P	18-Aug P	28-Aug P	08-Sep P
08-Apr	0.0304	***0.0138***	0.0327	0.8379	0.9743	0.8251	0.9893	0.8752	0.8937	0.1794	0.6625	0.8693
18-Apr	0.1083	***0.0015***	***0.0005***	0.6417	0.9833	0.8112	0.8972	0.9885	0.9241	0.6998	0.3381	0.8489
28-Apr	***0.0087***	0.992	0.914	0.6724	0.0581	0.997	0.5225	***0.0006***	0.043	***0.0024***	***0.0054***	0.1065
08-May	0.9928	0.3633	0.4356	0.0447	0.2694	0.3119	0.5127	0.7709	0.7874	0.9738	0.4461	0.7702
18-May	0.9357	0.9671	0.994	0.7139	0.6626	0.4324	0.1864	0.8	0.991	0.9958	0.8985	0.6817
28-May	0.9977	0.1012	0.209	0.639	0.982	0.3371	0.6062	0.9993	0.9958	0.967	0.9928	0.8238
08-Jun	0.9978	***0.0017***	***0.0074***	***0.0039***	0.4799	0.3026	0.2086	0.6834	0.0537	0.9632	0.5363	0.3045
18-Jun	0.9988	0.0365	0.807	0.6534	0.9977	0.1444	0.8699	0.9895	0.8423	0.9978	0.9999	0.4205
28-Jun	0.746	0.7618	0.8549	0.3704	0.5938	0.3818	0.3631	0.5118	***0.0247***	0.8302	0.7595	0.0497
08-Jul	0.9923	0.88	0.2133	0.0449	0.0415	0.1333	0.2812	0.0991	***0.0015***	0.6085	0.6361	0.2035
18-Jul	0.1842	0.9919	0.0668	***0.0207***	***0.0001***	0.5439	0.0688	***0.0001***	***0.0001***	***0.0062***	***0.0001***	0.4236
28-Jul	***0.0003***	0.966	0.0872	0.5128	***0.0058***	0.75	0.9824	***0.0001***	***0.0001***	***0.0001***	***0.0001***	0.3178
08-Aug	***0.001***	0.9999	0.9506	0.9948	0.3356	0.761	0.7969	0.0351	***0.001***	***0.0001***	***0.0009***	0.1357
18-Aug	***0.0001***	0.9999	0.9994	0.9998	0.5818	0.8979	0.7581	0.1236	0.5083	***0.0002***	0.0416	0.2325
28-Aug	***0.0001***	0.9843	0.9799	0.9972	0.3039	0.7881	0.5272	0.2946	0.2549	0.1096	0.0937	0.1632
08-Sep	0.5614	0.3371	0.7238	0.599	0.8026	0.7897	0.8728	0.5849	0.7571	0.7483	0.7314	0.1742
18-Sep	0.2224	0.7276	0.4877	0.5814	0.2239	0.8484	0.3492	0.2766	0.1587	0.367	0.3735	0.4255
28-Sep	0.094	0.9205	0.8593	0.9801	0.8992	0.5224	0.799	0.7585	0.4793	0.143	0.9277	0.1063
10-Oct	0.0434	0.944	0.9456	0.9894	0.9787	0.9291	0.9186	0.6144	0.4989	0.0217	0.912	***0.0174***

Table 22 - Results of interspecific association test (Perry & Dixon, 2002) between *T. tabaci* and *orius* spp. populations in GH3 during 2012. Grey cells indicate association test performed on spatial patterns observed in the same date.

Orius spp.

T. tabaci date	28-Jun P	08-Jul P	18-Jul P	28-Jul P	18-Aug P	28-Aug P	08-Sep P	18-Sep P	28-Sep P
08-Apr	0.9115	0.2568	0.2551	0.0448	0.8637	0.2909	-	0.475	0.5358
18-Apr	0.798	0.519	0.1694	***0.0162***	0.761	0.1691	0.8815	0.7557	0.8578
28-Apr	0.0323	***0.0009***	***0.0056***	0.8974	***0.0002***	***0.0069***	0.2529	0.3799	0.29
08-May	0.5897	0.514	0.4426	0.7732	0.3341	0.3421	0.6903	0.6662	0.5886
18-May	0.8852	0.9827	0.9969	0.9988	0.8181	0.9907	0.7453	0.6573	0.6003
28-May	0.9028	0.9956	0.9935	0.77	0.9941	0.964	0.8504	0.5151	0.5574
08-Jun	0.7372	0.6843	0.4853	***0.0011***	0.9231	0.916	0.4473	0.3657	0.4716
18-Jun	0.9946	0.9999	0.9999	0.5741	0.9999	0.9999	0.7132	0.7886	0.6233
28-Jun	0.8113	0.9775	0.9716	0.7023	0.9067	0.9679	0.6439	0.8476	0.7602
08-Jul	0.1634	0.3007	0.346	0.7592	0.0522	0.3239	0.126	0.1176	0.0932
18-Jul	***0.0001***	***0.0001***	***0.0001***	0.4659	***0.0001***	***0.0022***	***0.0012***	***0.0001***	***0.0004***
28-Jul	***0.0001***	***0.0001***	***0.0001***	0.2906	***0.0001***	***0.0051***	0.0887	0.1409	0.1048
08-Aug	0.038	***0.0001***	***0.0053***	0.9839	***0.0001***	***0.0074***	0.2479	0.1817	0.0764
18-Aug	0.187	***0.0223***	0.0871	0.9995	***0.0003***	***0.0084***	0.4008	0.5365	0.3909
28-Aug	0.274	***0.023***	0.0436	0.9034	***0.0144***	0.3146	0.0485	0.1309	0.0643
08-Sep	0.7524	0.815	0.8581	0.4588	0.7703	0.9161	0.9098	0.9826	0.9663
18-Sep	0.0336	0.056	0.0735	0.6826	***0.0242***	0.2474	0.3845	0.3852	0.3741
28-Sep	0.8858	0.6576	0.7432	0.8748	0.5547	0.6689	0.2122	0.177	0.1536
10-Oct	0.6668	0.4752	0.5883	0.8633	0.2811	0.5065	0.1205	0.0513	***0.0062***

In the open field nursery, observations started in June. *F. occidentalis* was detected from June onwards showing maximum densities in September (Figure 5). In the nursery, populations showed to be aggregated in mid-June and late September (Table 24). Females were rarely detected in the hedgerow (Figure 5). Similarities in thrips spatial distribution were found in late July (Table 25).

Table 23 - Results of interspecific association test (Perry & Dixon, 2002) between *Aeolothrips* spp. and *Orius* spp. populations in GH3 during 2012. Grey cells indicate association test performed on spatial patterns observed in the same date.

Aeolothrips spp.	*Orius* spp.								
date	**28-Jun** *P*	**08-Jul** *P*	**18-Jul** *P*	**28-Jul** *P*	**18-Aug** *P*	**28-Aug** *P*	**08-Sep** *P*	**18-Sep** *P*	**28-Sep** *P*
28-Apr	0,4888	***0,0073***	***0,0055***	0,8597	0,0384	0,083	0,0891	0,0934	0,0438
08-May	0,8447	0,9712	0,7083	***0,0001***	0,9999	0,9845	0,8302	0,8708	0,9554
08-Jun	***0,0116***	***0,0048***	***0,0001***	***0,0001***	0,3007	0,0891	0,4324	0,3067	0,5351
18-Jun	***0,006***	0,092	0,0445	***0,0004***	0,1407	0,2419	0,4354	0,5438	0,7156
28-Jun	***0,0001***	***0,0001***	***0,0001***	0,06	***0,0001***	***0,0031***	0,0926	0,0691	0,1212
08-Jul	0,049	0,5985	0,6646	0,2839	0,4104	0,3467	0,5484	0,7909	0,8195
18-Jul	***0,0066***	0,249	0,3379	0,8122	0,0519	***0,0056***	0,1891	0,1659	0,2393
28-Jul	***0,0001***	***0,0001***	***0,0001***	0,1355	***0,0001***	***0,0064***	0,0411	0,0861	0,0443
08-Aug	***0,007***	***0,0004***	***0,0003***	0,6047	***0,0009***	0,0389	0,0594	0,0422	***0,0221***
18-Aug	***0,0038***	***0,0001***	***0,0001***	0,6502	***0,0001***	***0,0001***	0,0804	***0,0055***	***0,0045***
28-Aug	***0,0001***	***0,0001***	***0,0001***	0,3353	***0,0001***	***0,0001***	0,3937	0,3724	0,4275
08-Sep	0,3408	0,4205	0,4915	0,9345	0,2139	0,0538	***0,0001***	0,079	***0,004***

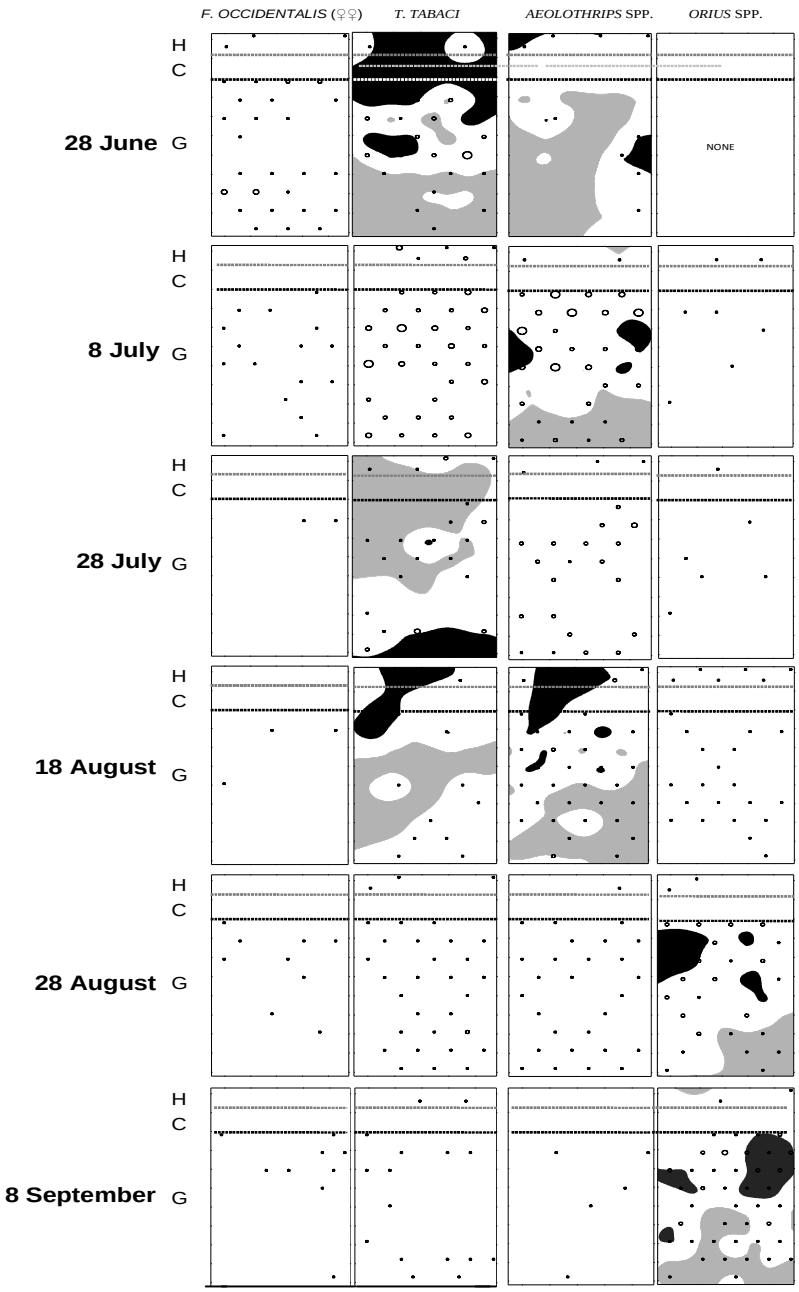

Figure 6 - Spatial patterns of *F. occidentalis*, *T. tabaci*, *Aeolothrips* spp., *Orius* spp. populations in the greenhouse OFN on selected sampling dates during 2012. Black areas correspond to patch ($v_i > 1.5$) whilst grey correspond to gap ($v_j < -1.5$). Letters 'H', 'C', 'G' indicate 'hedgerow', 'corridor', and 'greenhouse' respectively. Points inside or outside greenhouse correspond to locations of traps with insect capture .

Table 24 - Aggregation index (I) and associated probability (p) of *F. occidentalis*, *T. tabaci*, *Aeolothrips* spp. and *Orius* spp. populations in greenhouse OFN and its surroundings during 2012.

OFN

date	*F. occidentalis* (♀♀)		*T. tabaci*		*Aeolothrips* spp.		*Orius* spp.	
	I	**P**	**I**	**P**	**I**	**P**	**I**	**P**
08-apr	-	-	-	-	-	-	-	-
18-apr	-	-	-	-	-	-	-	-
28-apr	-	-	-	-	-	-	-	-
08-mag	-	-	-	-	-	-	-	-
18-May	-	-	-	-	-	-	-	-
28-May	-	-	-	-	-	-	-	-
8-June	-	-	-	-	-	-	-	-
18-June	***1.512***	***0.0243***	1,358	0.0657	0.948	0.5112	-	-
28-June	1.021	0.3709	***2,388***	***0.0003***	***1.807***	***0.0018***	-	-
8-July	1.026	0.3488	1,078	0.2754	***1.492***	***0.0256***	0.946	0.5158
18-July	1.4	0.0528	1,184	0.166	1.32	0.0743	-	-
28-July	1.152	0.2025	***1.796***	***0.0024***	1.082	0.2575	0.896	0.6557
8-Aug	-	-	-	-	-	-	-	-
18-Aug	0.946	0.5053	***1.644***	***0.0101***	***1.909***	***0.0024***	1,324	0.0745
28-Aug	1.138	0.191	1.271	0.1159	1.084	0.2537	***1.418***	***0.0406***
8-Sept	1.241	0.1042	0.899	0.6859	0.784	0.9292	***1.527***	***0.0174***
18-Sep	1.199	0.1343	***1.698***	***0.0075***	1.291	0.1018	1.291	1.171
28-Sep	***1.672***	***0.0049***	1.284	0.0816	1.174	0.1549	1.174	-
8-Oct	1.335	0.0614	1.283	0.0875	0.778	0.9013	0.778	-

Table 25 - Results of association test (Perry & Dixon, 2002) of *F. occidentalis* populations in greenhouse OFN during 2012.

		F. occidentalis (♀♀)						
	date	**08-Jul** *P*	**18-Jul** *P*	**28-Jul** *P*	**18-Aug** *P*	**28-Aug** *P*	**08-Sep** *P*	**18-Sep** *P*
F. occidentalis (♀♀)	**28-Jun**	0.8065	0.9114	0.8064	0.4476	0.9136	0.9245	0.5244
	18-Jun	0.3588	0.5404	0.9997	0.7549	0.8169	0.4321	0.0282
	08-Jul		0.0389	0.5087	0.354	0.1682	0.7263	***0.0091***
	18-Jul			0.0879	***0.0124***	0.0276	-	-
	28-Jul				***0.0003***	***0.0001***	0.0462	0.7725
	18-Aug					0.0324	***0.0159***	0.8155
	28-Aug						0.0609	0.257
	18-Sep							

The population of *T. tabaci* was frequently found in the rose nursery as well as in the contiguous hedgerow (Figure 6). Populations densities peaked in June and July. Aggregative patterns involved both the hedgerow and the nursery in late June and mid-August while only the nursery in late July and mid-September (Table 24; Figure 6). Intraspecific associations resulted not significant.

Predaceous thrips were also observed in both the nursery and the hedgerow where populations were aggregated in late June and mid-August (Table 24; Figure 6). An additional aggregative pattern was seen in the hedgerow in early July. Population densities peaked in July and August (Figure 6). Intraspecific association showed to be significant in the first half of July (Table 26).

Table 26 - Results of association test (Perry & Dixon, 2002) of *Aeolothrips* spp. populations in greenhouse OFN during 2012.

Aeolothrips spp.	date	28-Jun	08-Jul	18-Jul	28-Jul	18-Aug	28-Aug	08-Sep
		P	*P*	*P*	*P*	*P*	*P*	*P*
Aeolothrips spp.	18-Jun	0.1915	0.7354	0.7252	0.3967	0.1167	0.8433	0.9788
	28-Jun		0.5396	0.2921	0.8992	0.4008	0.9648	0.9215
	08-Jul			***0.0004***	0.0381	0.1137	0.0776	0.1682
	18-Jul				0.5442	0.0523	0.8183	-
	28-Jul					0.836	***0.0001***	0.2096
	18-Aug						0.7619	0.9879
	28-Aug							0.2595
	08-Sep							

Table 27- Results of interspecific association test (Perry & Dixon, 2002) between *F. occidentalis* and *T. tabaci* populations in OFN during 2012. Grey cells indicate association test performed on spatial patterns observed in the same date.

T. tabaci	date	18-Jun	28-Jun	08-Jul	18-Jul	28-Jul	18-Aug	28-Aug	08-Sep
		P	*P*	*P*	*P*	*P*	*P*	*P*	*P*
F. occidentalis (♀♀)	18-Jun	0.5185	0.9999	0.838	0.8125	0.097	0.9999	0.012	0.9212
	28-Jun	0.9449	0.6928	0.6662	0.8588	0.7008	0.8594	0.195	0.5337
	08-Jul	***0.0178***	0.3602	***0.0243***	0.0497	0.8809	0.7732	0.8939	0.9369
	18-Jul	***0.0158***	***0.0088***	0.0889	***0.0011***	0.9977	0.9255	0.9916	-
	28-Jul	***0.0222***	***0.0001***	0.0381	***0.0009***	0.9965	0.2655	0.9999	0.3674
	18-Aug	0.0335	***0.0075***	***0.0082***	***0.0002***	0.9983	0.9179	0.9997	0.421
	28-Aug	***0.0009***	0.0931	0.1961	0.0325	0.9584	0.6322	0.885	0.6951
	08-Sep	0.0839	0.7537	0.3094	-	0.2141	0.855	0.7141	0.5323
	18-Sep	0.2182	0.7429	0.0119	-	0.358	0.8873	0.572	0.9537

Predatory bugs were commonly observed inside the rose nursery and less frequently in the hedgerow (Figure 6). Population densities peaked at the end of summer when significant spatial patterns occurred inside the nursery (Table 24; Figure 6). Intraspecific spatial analysis revealed no significant similarities in the distribution of *Orius* population

among sampling dates.

Significant interspecific associations were found between *F. occidentalis* and *T. tabaci* in July (Table 27). Significant associations inside the nursery involved *F. occidentalis* and predatory thrips (Table 28), but especially *F. occidentalis* and *Orius* spp. (Table 29). Additional associations were reported between *T. tabaci* and predatory thrips (Table 30) or *Orius* spp. (Table 31). *Aeolothrips* spp. was also positively associated with *Orius* spp. in July, August and September (Table 32).

Table 28 - Results of interspecific association test (Perry & Dixon, 2002) between *F. occidentalis* and *Aeolothrips* spp. populations in OFN during 2012. Grey cells indicate association test performed on spatial patterns observed in the same date.

		Aeolothrips spp.								
	date	**18-Jun**	**28-Jun**	**08-Jul**	**18-Jul**	**28-Jul**	**18-Aug**	**28-Aug**	**08-Sep**	**18-Sep**
		P	*P*	*P*	*P*	*P*	*P*	*P*	*P*	*P*
F. occidentalis (♀♀)	**18-Jun**	0.7505	0.9999	0.8813	0.8732	0.1477	0.9869	0.1746	0.0504	0.0193
	28-Jun	0.8948	0.9467	0.8562	0.6039	0.7886	0.4862	0.7576	0.6416	0.4371
	08-Jul	0.6167	0.8785	***0.0064***	0.2548	0.098	0.8619	0.0898	0.2313	0.2294
	18-Jul	0.7702	0.3019	***0.0001***	***0.0009***	0.5358	0.0322	0.3335	-	-
	28-Jul	0.1723	0.0842	***0.0001***	***0.0003***	0.1245	***0.0021***	0.1559	0.8017	0.9969
	18-Aug	0.5421	0.7116	***0.0001***	***0.0015***	0.2008	0.0356	0.0662	0.7796	0.979
	28-Aug	0.1056	0.5546	***0.007***	***0.0016***	***0.0233***	0.3039	0.2667	0.5105	0.9741
	08-Sep	0.7561	0.5633	0.354	-	0.1696	0.8252	0.1169	0.0275	0.9999
	18-Sep	0.8823	0.9788	0.1998	-	0.1916	0.8962	0.1721	***0.0229***	0.9948

Table 29 - Results of interspecific association test (Perry & Dixon, 2002) between *F. occidentalis* and *Orius* spp. populations in OFN during 2012. Grey cells indicate association test performed on spatial patterns observed in the same date.

F. occidentalis (♀♀) \ *Orius* spp.	08-Jul	28-Jul	18-Aug	28-Aug	08-Sep	18-Sep
date	*P*	*P*	*P*	*P*	*P*	*P*
18-Jun	0.7922	0.5456	0.8408	0.5967	0.0657	0.0141
28-Jun	0.5338	0.6506	0.2727	0.7327	0.2213	0.4185
08-Jul	0.2785	0.4931	0.9834	0.0572	0.1622	0.2232
18-Jul	***0.0098***	0.0122	0.8822	***0.0045***	-	-
28-Jul	0.0764	***0.0186***	0.622	***0.0049***	0.9404	0.9956
18-Aug	***0.0177***	***0.0199***	0.8991	***0.0001***	0.9452	0.98
28-Aug	0.4629	0.4408	0.7657	***0.0119***	0.8484	0.9827
08-Sep	0.5666	0.5239	0.5909	0.1105	***0.0211***	0.9973
18-Sep	0.4558	0.7721	0.7635	0.7552	***0.0004***	0.9361

Table 30 - Results of interspecific association test (Perry & Dixon, 2002) between *T. tabaci* and *Aeolothrips* spp. populations in OFN during 2012. Grey cells indicate association test performed on spatial patterns observed in the same date.

T. tabaci \ *Aeolothrips* spp.	18-Jun	28-Jun	08-Jul	18-Jul	28-Jul	18-Aug	28-Aug	08-Sep	18-Sep
date	*P*	*P*	*P*	*P*	*P*	*P*	*P*	*P*	*P*
18-Jun	0.6226	0.703	***0.0067***	0.0352	***0.0021***	0.143	***0.015***	0.222	0.7977
28-Jun	0.1306	0.0735	***0.0001***	***0.009***	0.9243	***0.0062***	0.9539	0.7678	0.9508
08-Jul	0.8849	0.6721	***0.0054***	0.0356	0.085	0.5643	0.0668	0.1931	0.508
18-Jul	0.7369	0.2886	***0.0004***	***0.0002***	0.6803	0.0376	0.135	-	-
28-Jul	0.2269	0.6577	0.9998	0.9949	0.1664	0.9929	0.4521	0.4042	0.2107
18-Aug	***0.0176***	***0.0038***	0.7912	0.308	0.9668	0.0352	0.9959	0.9728	0.6019
28-Aug	0.8469	0.3613	0.9948	0.9343	0.8064	0.9959	0.9718	0.3997	0.2823
08-Sep	0.1118	0.2412	0.8225	-	0.7498	0.0219	0.5655	0.9507	0.1525
18-Sep	0.7652	0.3452	0.9686	-	0.3243	0.6632	0.2899	0.9349	***0.0001***

Table 31 - Results of interspecific association test (Perry & Dixon, 2002) between *T. tabaci* and *Orius* spp. populations in OFN during 2012. Grey cells indicate association test performed on spatial patterns observed in the same date.

T. tabaci	*Orius* spp.					
date	**08-Jul**	**28-Jul**	**18-Aug**	**28-Aug**	**08-Sep**	**18-Sep**
	P	*P*	*P*	*P*	*P*	*P*
18-Jun	0.3319	0.1708	0.9305	***0.0001***	0.5767	0.8557
28-Jun	***0.0041***	0.0284	0.1794	0.0504	0.9432	0.9437
08-Jul	0.4656	0.648	0.8757	0.1328	0.3585	0.4909
18-Jul	***0.0001***	0.0651	0.4228	***0.0001***	-	-
28-Jul	0.9985	0.9572	0.5335	0.9999	0.171	0.1877
18-Aug	0.6367	0.3775	0.0821	0.8682	0.569	0.59
28-Aug	0.9627	0.8579	0.1506	0.9684	0.6624	0.3496
08-Sep	0.2137	0.1651	0.2516	0.4915	0.7511	0.1715
18-Sep	0.8859	0.9858	0.5446	0.9226	0.9999	***0.0001***

Table 32 - Results of interspecific association test (Perry & Dixon, 2002) between *Aeolothrips* spp. and *Orius* spp. populations in OFN during 2012. Grey cells indicate association test performed on spatial patterns observed in the same date.

Aeolothrips spp.	*Orius* spp.					
date	**08-Jul**	**28-Jul**	**18-Aug**	**28-Aug**	**08-Sep**	**18-Sep**
	P	***P***	***P***	***P***	***P***	***P***
18-Jun	0.3529	0.9114	0.4228	0.6178	0.5024	0.6108
28-Jun	0.6994	0.4612	***0.0239***	0.7173	0.8313	0.8224
08-Jul	***0.0157***	***0.0015***	***0.9883***	***0.0003***	0.7539	0.8376
18-Jul	0.0405	***0.0167***	0.2879	***0.0069***	-	-
28-Jul	0.9237	0.2548	**0.9998**	0.0592	0.0595	0.1525
18-Aug	0.0317	***0.0044***	0.1568	0.0504	0.6073	0.6513
28-Aug	0.7717	0.5619	0.998	***0.0223***	0.1098	0.2342
08-Sep	0.3138	0.9078	0.8007	0.7662	0.135	0.8682
18-Sep	0.902	***0.9784***	0.8644	0.9772	**0.9998**	***0.0001***

Spatial and temporal dynamics in 2013

F. occidentalis was commonly detected in the greenhouse GH1, less frequently in the contiguous hedgerow (Figure 7). Thrips numbers in the greenhouse increased from April to July, then declined probably because of plant cutting practices. Population were strongly aggregated inside greenhouse from late June to early August with hotspots in correspondence of the southern side and gaps in the area facing the hedgerow (Table 33; Figure 7). A strong similarity among population distribution was observed in a number of sampling dates (Table 34).

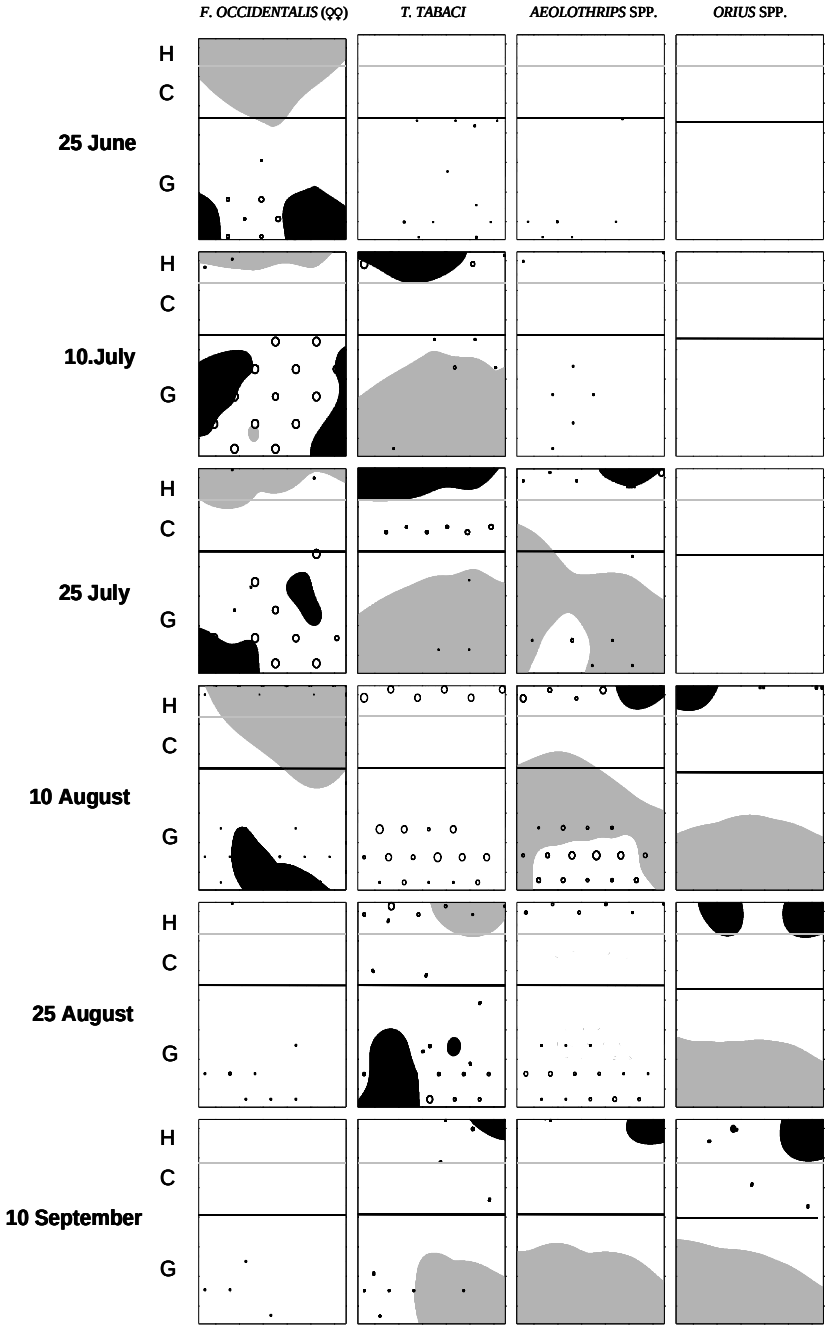

Figure 7 - Spatial patterns of *F. occidentalis*, *T. tabaci*, *Aeolothrips* spp., *Orius* spp. populations in the greenhouse GH1 on selected sampling dates during 2013. Black areas correspond to patch ($v_i > 1.5$) whilst grey correspond to gap ($v_j < -1.5$). Letters 'H', 'C', 'G' indicate 'hedgerow', 'corridor', and 'greenhouse' respectively. Points inside or outside greenhouse correspond to locations of traps with insect captures.

Table 33 - index (I) and associated probability (p) of *F. occidentalis*, *T. tabaci*, *Aeolothrips* spp. and *Orius* spp. populations in greenhouse GH1 and its surroundings during 2013.

GH1

date	*F. occidentalis* (♀♀)		*T. tabaci*		*Aeolothrips* spp.		*Orius* spp.	
	I	P	I	P	I	P	I	P
10-apr	1.047	0.4752	0.774	0.9816	-	-	-	-
25-apr	0.889	0.6635	-	-	-	-	-	-
10-May	1.033	0.367	0.907	0.6867	0.857	0.7171	-	-
25-May	1.241	0.1178	1.076	0.2236	-	-	-	-
10-June	1.229	0.1122	0.969	0.4968	-	-	-	-
25-June	***1.752***	***0.0008***	0.914	0.6146	1.04	0.3654	-	-
10-July	***1.704***	***0.004***	***2.13***	***0.0008***	1.256	0.0986	-	-
25-July	***1.678***	***0.0024***	***2.126***	***0.0008***	***1.553***	***0.0128***	-	-
10-Aug	***1.638***	***0.0176***	1.282	0.1386	***1.483***	***0.0401***	***1.949***	***0.0008***
25-Aug	1.266	0.1226	***1.788***	***0.0072***	0.967	0.488	***2.07***	***0.0008***
10-Sept	1.314	0.0865	***1.528***	***0.0313***	***1.953***	***0.0032***	***1.951***	***0.0008***

Table 34 - Results of association test (Perry & Dixon, 2002) of *F. occidentalis* populations in greenhouse GH1 during 2013.

F. occidentalis (♀♀)

F. occidentalis (♀♀) date	25-Apr P	10-May P	25-May P	10-Jun P	25-Jun P	10-Jul P	25-Jul P	10-Aug P	25-Aug P	10-Sep P
10-Apr	0.8965	***0.0059***	0.3403	0.6051	***0.002***	***0.0194***	0.2597	0.2192	0.222	0.1345
25-Apr		0.9231	0.059	0.0793	0.303	0.6977	0.1771	0.2752	0.2705	0.3623
10-May			0.2835	0.6658	0.0157	0.1457	0.2831	0.7472	0.7844	0.7431
25-May				***0.0022***	0.0425	0.3234	0.0729	0.0846	***0.0245***	0.1358
10-Jun					0.2119	0.1223	0.0345	***0.0113***	***0.023***	0.1132
25-Jun						***0.0093***	***0.0062***	0.135	0.1498	0.0308
10-Jul							0.2257	0.3288	0.331	0.2926
25-Jul								0.15	0.15	0.1385
10-Aug									***0.0007***	***0.0117***
25-Aug										***0.0006***
10-Sep										

T. tabaci was rarely detected in spring. Populations were aggregated in July and September in the hedgerow, from late August to early September inside the greenhouse (Table 33; Figure7). A similarity between the spatial distributions of *T. tabaci* population was observed in July (Table 35).

Table 35 - Results of association test (Perry & Dixon, 2002) for of *T. tabaci* populations in greenhouse GH1 during 2013.

		T. tabaci								
	date	10-May	25-May	10-Jun	25-Jun	10-Jul	25-Jul	10-Aug	25-Aug	10-Sep
		P	*P*	*P*	*P*	*P*	*P*	*P*	*P*	*P*
T. tabaci	10-Apr	0.2894	0.1051	0.1861	0.755	0.9739	0.9623	0.8499	0.15	0.4529
	10-May		0.3384	***0.0032***	0.9561	0.8985	0.9247	0.8544	0.0767	0.9114
	25-May			0.3896	0.3687	0.9999	0.9999	0.8499	0.1444	0.7549
	10-Jun				0.9571	0.7976	0.7675	0.8499	0.099	0.7612
	25-Jun					0.2364	0.1995	0.4024	0.5465	0.2522
	10-Jul						***0.0001***	0.15	0.8234	0.4782
	25-Jul							0.15	0.8499	0.5186
	10-Aug								0.7958	0.0334
	25-Aug									0.2204
	10-Sep									

Predaceous thrips were rarely detected until mid-July inside and outside the greenhouse (Figure7). Then populations increased and showed to be aggregated in the hedgerow in late July, early August and early September (Table 33; Figure7). Gaps were located in the side of GH2 facing to other greenhouses. Intraspecific association did not evidence significant patterns.

Anthocorids were detected only in the hedgerow where populations were aggregated from early August to early September (Table 33; Figure7). A stable spatial structure was evidenced in August (Table 36).

Table 36 - Results of association test (Perry & Dixon, 2002) of *Orius* spp. populations in greenhouse GH1 during 2013.

		Orius spp.	
	date	25-Aug	10-Sep
		P	*P*
Orius spp.	10-Aug	***0.0001***	***0.0002***
	25-Aug		***0.0001***

F. occidentalis and *T. tabaci* populations were found to be positively associated between May and June inside the greenhouse (Table 37). Positive associations between *F. occidentalis* and *Aeolothrips* species populations were observed in early May and late June inside the greenhouse, in late August in correspondence of the hedgerow (Table 38). Additional positive associations were detected between *T. tabaci* and *Aeolothrips* spp. in early August (Table 39), and between *T. tabaci* and *Orius* spp. in early August and early September (Table 40). These associations occurred in the hedgerow. Similar trends were seen regarding the association between *Aeolothrips* spp. and *Orius* spp. populations (Table 41).

Table 37 - Results of interspecific association test (Perry & Dixon, 2002) between *F. occidentalis* and *T. tabaci* populations in GH1 during 2013. Grey cells indicate association test performed on spatial patterns observed in the same date.

		T. tabaci									
	date	**10-Apr**	**10-May**	**25-May**	**10-Jun**	**25-Jun**	**10-Jul**	**25-Jul**	**10-Aug**	**25-Aug**	**10-Sep**
		P	***P***	***P***	***P***	***P***	***P***	***P***	***P***	***P***	***P***
F. occidentalis (♀♀)	**10-Apr**	0.5123	0.324	0.0891	0.7109	0.2776	0.9978	0.996	0.7707	0.3073	0.2931
	25-Apr	0.2215	0.64	0.1262	0.4269	0.3859	0.5317	0.6591	0.7627	0.0856	0.7672
	10-May	0.3778	0.3751	0.4025	0.7673	0.6413	0.9734	0.9547	0.2804	0.9416	0.0318
	25-May	0.0454	0.2582	***0.0073***	0.1478	0.8752	0.9999	0.9999	0.8499	0.1322	0.7672
	10-Jun	0.1143	0.2732	***0.0153***	***0.0118***	0.8455	0.9905	0.9948	0.8499	0.15	0.6895
	25-Jun	0.4013	0.3441	***0.0062***	0.5845	0.4402	0.9999	0.9999	0.8536	0.2194	0.5344
	10-Jul	0.3563	0.1217	0.099	0.1659	0.7305	0.9848	0.9847	0.6728	0.6606	0.2537
	25-Jul	***0.0194***	0.0801	0.0237	0.0883	0.6793	0.9973	0.9947	0.8544	0.15	0.569
	10-Aug	0.15	0.15	0.0616	0.0836	0.5113	0.8535	0.8499	0.9817	0.1281	0.9869
	25-Aug	0.15	0.1494	***0.019***	0.1222	0.5694	0.8499	0.8499	0.9797	0.0325	0.6419
	10-Sep	0.1499	0.1466	0.143	***0.0077***	0.4232	0.9557	0.8499	0.7929	0.0115	0.3261

Table 38 - Results of interspecific association test (Perry & Dixon, 2002) between *F. occidentalis* and *Aeolothrips* spp. populations in GH1 during 2013. Grey cells indicate association test performed on spatial patterns observed in the same date.

Aeolothrips spp.

F. occidentalis (♀♀) date	10-May *P*	25-Jun *P*	10-Jul *P*	25-Jul *P*	10-Aug *P*	25-Aug *P*	10-Sep *P*
10-Apr	0.0414	0.1827	0.9023	0.9609	0.0272	0.1245	0.7228
25-Apr	0.4427	0.0985	0.2237	0.1167	0.8423	0.3843	0.9751
10-May	***0.0025***	0.4654	0.941	0.9843	0.1126	0.4414	0.0779
25-May	***0.0051***	0.0862	***0.0087***	0.7553	0.4267	0.2867	0.9028
10-Jun	0.1676	0.0593	***0.0029***	0.6886	0.3573	0.2867	0.8712
25-Jun	***0.0001***	***0.0138***	0.464	0.9077	0.0638	0.2148	0.8758
10-Jul	0.1017	0.1882	0.5265	0.9431	0.0814	0.4351	0.4581
25-Jul	0.124	0.0427	0.2174	0.8457	0.2254	0.2215	0.9017
10-Aug	0.15	0.2049	0.1046	0.6406	0.6905	***0.002***	0.9999
25-Aug	0.15	0.2031	0.1193	0.6701	0.9016	***0.0026***	0.9998
10-Sep	0.15	0.1077	***0.014***	0.4604	0.9952	0.0862	0.9905

Table 39 - Results of interspecific association test (Perry & Dixon, 2002) between *T. tabaci* and *Aeolothrips* spp. populations in GH1 during 2013. Grey cells indicate association test performed on spatial patterns observed in the same date.

Aeolothrips spp.

T. tabaci date	10-May *P*	25-Jun *P*	10-Jul *P*	25-Jul *P*	10-Aug *P*	25-Aug *P*	10-Sep *P*
10-Apr	0.2394	0.1748	0.1425	0.6604	0.1534	0.1569	0.857
10-May	0.2712	0.7065	0.3376	0.998	0.6279	0.3095	0.986
25-May	0.0432	0.0712	0.1026	0.497	0.4086	0.2867	0.8801
10-Jun	0.5507	0.4674	0.0322	0.9456	0.3701	0.3637	0.8815
25-Jun	0.7115	0.185	0.7104	***0.0109***	0.0512	0.2755	0.3168
10-Jul	0.9999	0.9962	0.8869	0.0507	0.8752	0.7661	0.15
25-Jul	0.9999	0.9628	0.8263	0.0377	0.7575	0.7504	0.1394
10-Aug	0.8499	0.7824	0.8542	0.311	0.0941	0.8675	***0.0003***
25-Aug	0.15	0.2906	0.1969	0.4065	0.9507	0.4681	0.9867
10-Sep	0.5066	0.3459	0.6087	-	0.2926	0.8518	***0.0201***

Table 40 - Results of interspecific association test (Perry & Dixon, 2002) between *T. tabaci* and *Orius* spp. populations in GH1 during 2013. Grey cells indicate association test performed on spatial patterns observed in the same date.

		Orius spp.		
	date	10-Aug *P*	25-Aug *P*	10-Sep *P*
T. tabaci	10-Apr	0.8817	0.8499	0.8499
	10-May	0.8482	0.9056	0.9478
	25-May	0.8499	0.8499	0.8499
	10-Jun	0.8577	0.8576	0.8678
	25-Jun	0.5171	0.4931	0.4129
	10-Jul	0.1663	0.1656	0.1715
	25-Jul	0.15	0.15	0.15
	10-Aug	***0.0002***	***0.0003***	***0.0008***
	25-Aug	0.9715	0.9855	0.9951
	10-Sep	0.0277	0.0424	***0.0249***

Table 41 - Results of interspecific association test (Perry & Dixon, 2002) between *Aeolothrips* spp. and *Orius* spp. populations in GH1 during 2013. Grey cells indicate association test performed on spatial patterns observed in the same date.

		***Orius* spp.**		
	date	**10-Aug *P***	**25-Aug *P***	**10-Sep *P***
Aeolothrips spp.	**10-May**	0,8499	0,8499	0,8499
	25-Jun	0,8431	0,776	0,6897
	10-Jul	0,737	0,8525	0,8079
	25-Jul	0,6229	0,2863	0,3035
	10-Aug	0,135	0,1027	0,0585
	25-Aug	0,9982	0,9996	0,9973
	10-Sep	***0,0001***	***0,0001***	***0,0001***

In spring, *F. occidentalis* was detected at low population densities in the greenhouse GH2 and its surroundings (Figure 8). Populations increased in summer but declined from August onwards because most of flowering ornamentals were removed (Figure 8). No significant spatial patterns were observed for *F. occidentalis* females in this scenario (Table 42; Figure 8) but aggregation was seen for males in early May. A single case of intraspecific association among thrips female populations was observed in July (Table 43).

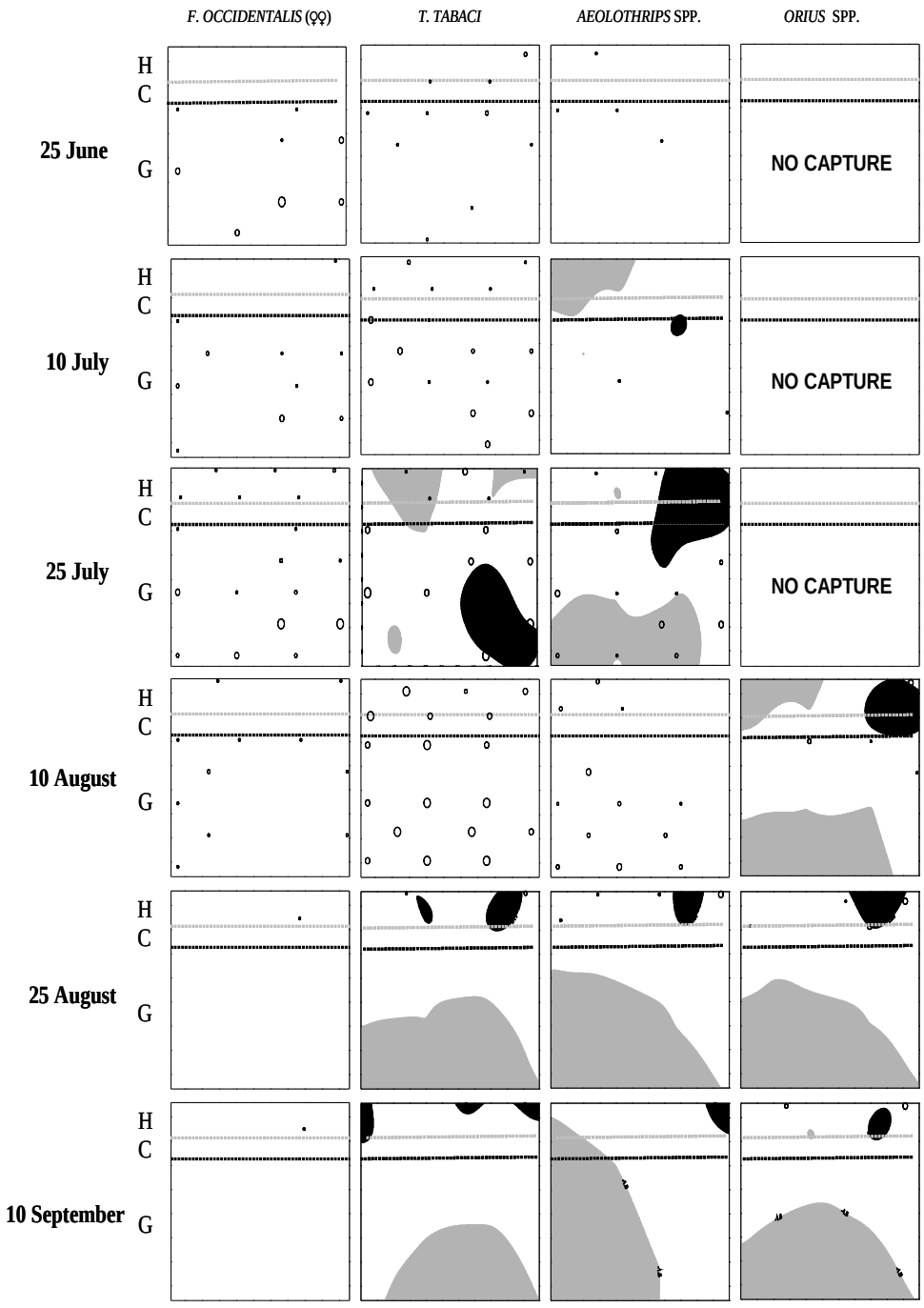

Figure 8 - Spatial patterns of *F. occidentalis*, *T. tabaci*, *Aeolothrips* spp., *Orius* spp. populations in the greenhouse GH2 on selected sampling dates during 2013. Black areas correspond to patch ($v_i > 1.5$) whilst grey correspond to gap ($v_j < - 1.5$). Letters 'H', 'C', 'G' indicate 'hedgerow', 'corridor', and 'greenhouse' respectively. Points inside or outside greenhouse correspond to locations of traps with insect captures.

Table 42 - Aggregation index (I) and associated probability (p) of *F. occidentalis*, *T. tabaci*, *Aeolothrips* spp. and *Orius* spp. populations in greenhouse GH2 and its surroundings during 2013.

GH2

date	*F. occidentalis* (♀♀)		*T. tabaci*		*Aeolothrips* spp.		*Orius* spp.	
	I	P	I	P	I	P	I	P
10-apr	1.023	0.4543	-	-	-	-	-	-
25-apr	0.878	0.7764	1.208	0.1803	0.904	0.7532	-	-
10-May	1.006	0.4111	1.271	0.0601	1.253	0.0697	-	-
25-May	0.889	0.754	0.986	0.5601	-	-	-	-
10-June	1.176	0.1595	0.974	0.4944	-	-	-	-
25-June	0.822	0.8638	1.308	0.0569	1.061	0.2949	-	-
10-July	1.023	0.3742	1.078	0.2692	1.045	0.3574	-	-
25-July	1.213	0.125	***1.361***	***0.0345***	***1.426***	***0.0224***	-	-
10-Aug	0.95	0.5633	0.843	0.8189	***1.476***	***0.012***	***1.565***	***0.004***
25-Aug	0.1529	0.1146	***1.403***	***0.0216***	***1.501***	***0.0032***	***1.48***	***0.012***
10-Sept	0.1529	0.1146	1.141	0.1923	***1.292***	***0.0457***	***1.39***	***0.0224***

Table 43 - Results of association test (Perry & Dixon, 2002) of *F. occidentalis* populations in greenhouse GH2 during 2013.

F. occidentalis (♀♀)

F. occidentalis (♀♀) date	10-May P	25-May P	10-Jun P	25-Jun P	10-Jul P	25-Jul P	10-Aug P	25-Aug P	10-Sep P
25-Apr	0.9606	0.3372	-	-	-	-	-	-	-
10-May		0.383	-	-	-	-	-	-	-
25-May			-	-	-	-	-	-	-
10-Jun				0.2534	0.0663	0.047	0.743	-	-
25-Jun					0.0306	***0.0205***	0.0823	0.7804	0.7804
10-Jul						***0.0014***	0.2093	0.6494	0.6494
25-Jul							0.675	0.6809	0.6809
10-Aug								0.7691	0.7691
25-Aug									-
10-Sep									

T. tabaci occurred at low levels in spring then captures increased until early August (Figure 8). Significant aggregations were observed in late July and late August (Table 42; Figure 8), the former occurring inside greenhouse and the latter in the hedgerow.

Similarities in the distribution of *T. tabaci* populations were observed in May, July and September (Table 43).

Table 44 - Results of association test (Perry & Dixon, 2002) of *T. tabaci* populations in greenhouse GH2 during 2013.

		T. tabaci								
	date	**10-May**	**25-May**	**10-Jun**	**25-Jun**	**10-Jul**	**25-Jul**	**10-Aug**	**25-Aug**	**10-Sep**
		P	*P*	*P*	*P*	*P*	*P*	*P*	*P*	*P*
T. tabaci	**25-Apr**	0.9399	0.9995	-	-	-	-	-	-	-
	10-May		***0.0237***	-	-	-	-	-	-	-
	25-May			-	-	-	-	-	-	-
	10-Jun				0.3502	0.0806	***0.0221***	0.245	-	-
	25-Jun					0.508	0.7019	0.6048	0.0365	0.0659
	10-Jul						***0.0161***	0.0567	0.9416	0.9288
	25-Jul							0.5891	0.9796	0.9768
	10-Aug								0.9583	0.955
	25-Aug									***0.0001***
	10-Sep									

*Aeolothrip*s spp. were detected in the greenhouse as well as in the hedgerow but their numbers increased in July (Figure 8). Populations were aggregated inside the greenhouse in late July, in both greenhouse and hedgerow in August, only in the hedgerow in September (Table 42; Figure 8). Intraspecific association was significant only in late summer (Table 45).

Table 45 - Results of association test (Perry & Dixon, 2002) for of *Aeolothrips* spp. populations in greenhouse GH2 during 2013.

		Aeolothrips spp.						
	date	**10-May**	**25-Jun**	**10-Jul**	**25-Jul**	**10-Aug**	**25-Aug**	**10-Sep**
		P	*P*	*P*	*P*	*P*	*P*	*P*
Aeolothrips spp.	**25-Apr**	0.9999	-	-	-	-	-	-
	10-May		-	-	-	-	-	-
	25-Jun			0.7631	0.5412	0.2863	0.1946	0.7555
	10-Jul				0.1281	0.9281	0.9462	0.7268
	25-Jul					0.1451	0.7529	0.2498
	10-Aug						0.0815	0.1501
	25-Aug							***0.0001***

Orius spp. were detected mostly in the hedgerow, sometimes inside the greenhouse (Figure 8). Populations were aggregated in late August when patches extended from the hedgerow to the first sector of the greenhouse (Table 42; Figure 8)). Additional aggregation patterns were noticed in the hedgerow in late August and early September (Table 42). A similarity in *Orius* spp. distributions was observed in late summer (Table 46).

Table 46 - Results of association test (Perry & Dixon, 2002) of *Orius* spp. populations in greenhouse GH2 during 2013.

		Orius spp.	
	date	**25-ago**	**10-set**
		P	*P*
Orius spp.	**10-Aug**	***0.0249***	***0.0131***
	25-Aug		***0.0009***

F. occidentalis and *T. tabaci* populations were positively associated in July inside the greenhouse and in September in the hedgerow (Table 47). *F. occidentalis* was associated with *Orius* spp. from 25 August to 10 September in the hedgerow (Table 48) whereas *F. occidentalis* and *Aeolothrips* spp. were never associated. *T. tabaci* was associated with *Aeolothrips* spp. in late August (Tables 49), and with *Orius* spp. in late August and early September (Table 50). Both situations occurred in the hedgerow where *Aeolothrips* spp. was associated with *Orius* spp. in late August and early September (Table 51).

Table 47 - Results of interspecific association test (Perry & Dixon, 2002) between *F. occidentalis* and *T. tabaci* populations in GH2 during 2013. Grey cells indicate association test performed on spatial patterns observed in the same date.

		T. tabaci									
	date	**25-Apr**	**10-May**	**25-May**	**10-Jun**	**25-Jun**	**10-Jul**	**25-Jul**	**10-Aug**	**25-Aug**	**10-Sep**
		P	***P***	***P***	***P***	***P***	***P***	***P***	***P***	***P***	***P***
F. occidentalis (♀♀)	**10-Apr**	0,9365	0,1042	0,0642	-	-	-	-	-	-	-
	25-Apr	0,1979	0,4909	0,4225	-	-	-	-	-	-	-
	10-May	0,334	0,3047	-	-	-	-	-	-	-	-
	25-May	0,2932	0,2353	0,1234	-	-	-	-	-	-	-
	10-Jun	-	-	-	0,2393	0,6831	0,1279	***0,0084***	0,0879	-	-
	25-Jun	-	-	-	0,19	0,5525	**0,0018**	0,1227	0,1053	0,9453	0,9262
	10-Jul	-	-	-	0,1958	0,5332	***0,007***	0,0146	0,2832	0,8933	0,9025
	25-Jul	-	-	-	0,3446	0,6677	***0,021***	0,0221	0,3804	0,9374	0,9505
	10-Aug	-	-	-	0,6926	0,145	0,0606	0,1462	0,789	0,3558	0,3782
	25-Aug	-	-	-	0,438	0,0726	0,7779	0,8928	0,8741	***0,0103***	***0,0001***
	10-Sep	-	-	-		0,438	0,0726	0,7779	0,8928	0,8741	***0,0015***

Table 48 - Results of interspecific association test (Perry & Dixon, 2002) between *F. occidentalis* and *Orius* spp. populations in GH2 during 2013. Grey cells indicate association test performed on spatial patterns observed in the same date.

F. occidentalis (♀♀)	*Orius* spp.		
date	**10-Aug** *P*	**25-Aug** *P*	**10-Sep** *P*
10-Jun	0.7173	0.9949	0.9987
25-Jun	0.694	0.9213	0.9434
10-Jul	0.5891	0.8102	0.8982
25-Jul	0.6412	0.9814	0.924
10-Aug	0.5397	0.5583	0.5493
25-Aug	0.0642	***0.0008***	***0.0042***
10-Sep	0.0666	***0.0001***	***0.0001***

Table 49 - Results of interspecific association test (Perry & Dixon, 2002) between *T. tabaci* and *Aeolothrips* spp. populations in GH2 during 2013. Grey cells indicate association test performed on spatial patterns observed in the same date.

T. tabaci	*Aeolothrips* spp.							
date	**25-Apr** *P*	**10-May** *P*	**25-Jun** *P*	**10-Jul** *P*	**25-Jul** *P*	**10-Aug** *P*	**25-Aug** *P*	**10-Sep** *P*
25-Apr	0.246	0.6278	-	-	-	-	-	-
10-May	0.9976	0.061	-	-	-	-	-	-
25-May	0.9463	0.1232	-	-	-	-	-	-
10-Jun	-	-	0.4491	0.379	0.3307	0.4332	0.6793	0.3733
25-Jun	-	-	0.7203	0.8687	0.2024	0.0822	0.047	0.0688
10-Jul	-	-	0.2404	0.1005	0.0641	0.6888	0.9469	0.7217
25-Jul	-	-	0.5501	0.0561	0.038	0.7143	0.9907	0.8285
10-Aug	-	-	0.5311	0.6174	0.688	0.5843	0.9605	0.8396
25-Aug	-	-	0.2117	0.9502	0.6458	0.0641	***0.0001***	0.2938
10-Sep	-	-	0.241	0.9558	0.6994	0.1114	0.3984	0.3334

Table 50 - Results of interspecific association test (Perry & Dixon, 2002) between *T. tabaci* and *Orius* spp. populations in GH2 during 2013. Grey cells indicate association test performed on spatial patterns observed in the same date.

T. tabaci	*Orius* spp.		
date	**10-Aug** *P*	**25-Aug** *P*	**10-Sep** *P*
10-Jun	0.6485	0.6319	0.6772
25-Jun	***0.004***	0.0501	0.0419
10-Jul	0.7553	0.9174	0.9239
25-Jul	0.6997	0.9542	0.9724
10-Aug	0.8556	0.924	0.9717
25-Aug	***0.0249***	***0.0001***	***0.0001***
10-Sep	0.0577	***0.0001***	***0.0001***

Table 51 - Results of interspecific association test (Perry & Dixon, 2002) between *Aeolothrips* spp. and *Orius* spp. populations in GH2 during 2013. Grey cells indicate association test performed on spatial patterns observed in the same date.

Aeolothrips spp.	*Orius* spp.		
date	**10-ago** ***P***	**25-ago** ***P***	**10-set** ***P***
10-lug	0.504	0.9583	0.9661
25-lug	0.0433	0.6794	0.5665
10-ago	0.0536	0.0679	0.0654
25-ago	0.0567	***0.0001***	***0.0001***
10-set	0.0422	***0.0001***	***0.0001***

In the first sampling dates, *F. occidentalis* was observed in the greenhouse GH3 rather than in its surroundings (Figure 9). Thrips captures inside the greenhouse increased in June and July. Population showed to be aggregated from early May onwards (Table 52; Figure 9). Hotspots location varied in space but most of them were located inside the greenhouse, sometimes outside but close to the main entries, localized in the northeastern corner. Gaps were located especially on the eastern and southern sides facing to the hedgerow and the orchard (Figure 9). Similarities in the distribution of thrips populations were found in all sampling dates (Table 53).

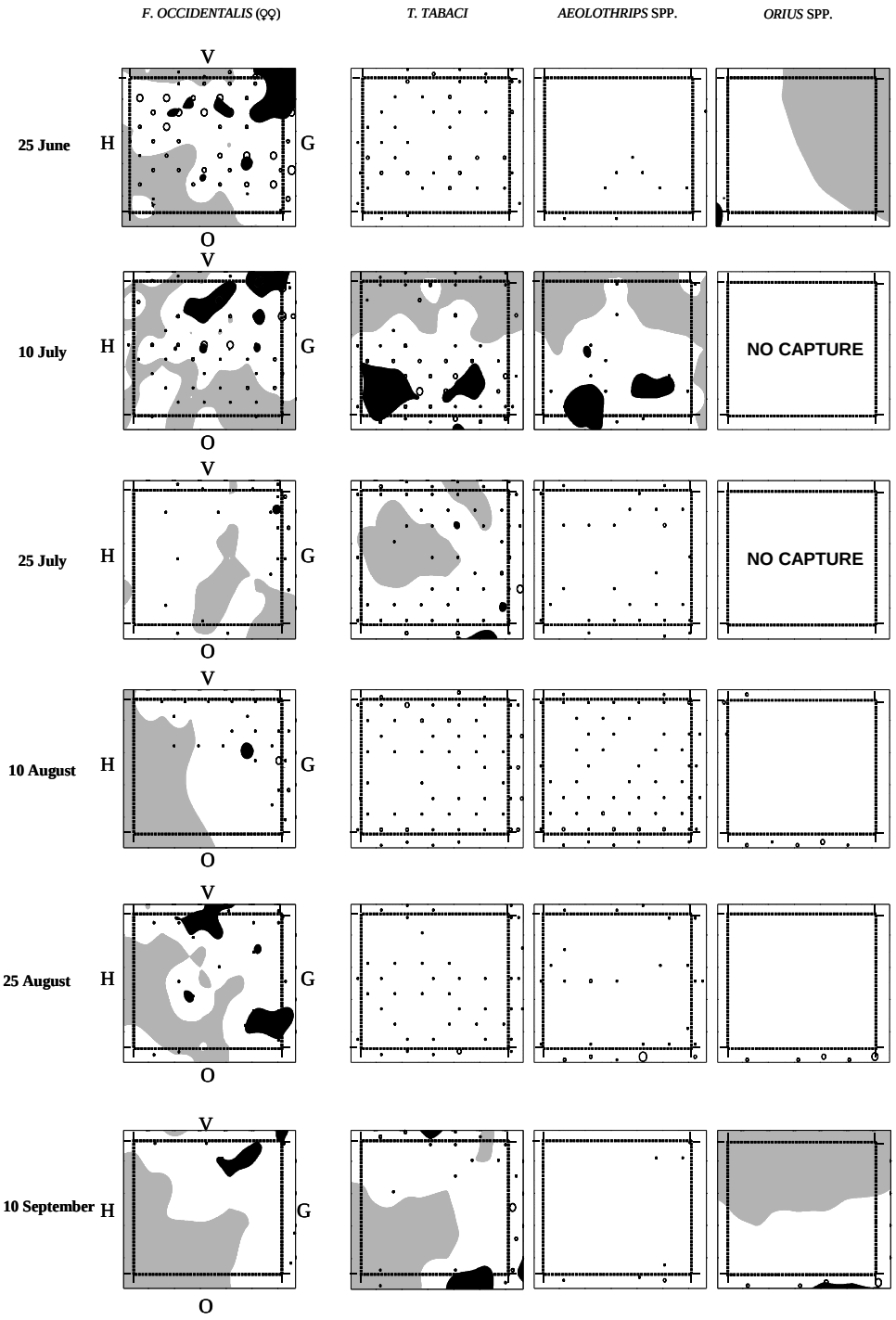

Figure 9 - Spatial patterns of *F. occidentalis*, *T. tabaci*, *Aeolothrips* spp., *Orius* spp. populations in the greenhouse GH3 on selected sampling dates during 2013. Black areas correspond to patch ($v_i > 1.5$) whilst grey correspond to gap ($v_j < - 1.5$). Letters 'H', 'C', 'G' indicate 'hedgerow', 'corridor', and 'greenhouse' respectively. Points inside or outside greenhouse correspond to locations of traps with insect captures.

Table 52 - Aggregation index (I) and associated probability (p) of *F. occidentalis*, *T. tabaci*, *Aeolothrips* spp. and *Orius* spp. populations in greenhouse GH3 and its surroundings during 2013.

GH3

date	*F. occidentalis* (♀♀)		*T. tabaci*		*Aeolothrips* spp.		*Orius* spp.	
	I	P	I	P	I	P	I	P
10-apr	1.18	0.1474	1.059	0.3902	-	-	1.063	0.3766
25-apr	1.291	0.0657	***1.342***	***0.0473***	-	-	-	-
10-May	***1.559***	***0.0096***	1.143	0.1827	-	-	1.172	0.1554
25-May	***1.327***	***0.0473***	0.91	0.6418	1.125	0.2051	-	-
10-June	***1.434***	***0.0248***	1.146	0.1851	0.909	0.6907	-	-
25-June	***1.953***	***0.0008***	0.875	0.7428	1.198	0.1258	***1.316***	***0.024***
10-July	***2.182***	***0.0008***	***1.782***	***0.0008***	***1.498***	***0.012***	-	-
25-July	***1.863***	***0.0008***	***1.418***	***0.0304***	1.122	0.2099	-	-
10-Aug	***1.432***	***0.0064***	1.062	0.2957	1.158	0.1603	1.301	0.0705
25-Aug	***1.616***	***0.0032***	1.279	0.0697	1.132	0.2228	***1.522***	***0.0096***
10-Sept	***1.583***	***0.008***	***1.475***	***0.0152***	1.273	0.0665	1.131	0.1907

Table 53 - Results of association test (Perry & Dixon, 2002) of *F. occidentalis* populations in greenhouse GH3 during 2013.

F. occidentalis (♀♀)

F. occidentalis (♀♀) date	25-Apr P	10-May P	25-May P	10-Jun P	25-Jun P	10-Jul P	25-Jul P	10-Aug P	25-Aug P	10-Sep P
10-Apr	***0.0004***	***0.0005***	***0.0071***	***0.0013***	***0.022***	***0.0163***	0.8792	0.6681	0.9612	***0.0583***
25-Apr		***0.0001***	***0.0001***	***0.0001***	***0.0001***	***0.0001***	***0.0074***	***0.0022***	0.0383	***0.0001***
10-May			***0.0001***	***0.0001***	***0.0001***	***0.0001***	0.0587	***0.0152***	0.8019	***0.006***
25-May				***0.0001***	***0.0001***	***0.0001***	0.0519	***0.0049***	0.3211	***0.001***
10-Jun					***0.0001***	***0.0004***	0.1444	***0.0098***	0.1349	***0.0001***
25-Jun						***0.0001***	***0.0001***	0.0255	0.0458	***0.0001***
10-Jul							***0.0009***	***0.0032***	***0.0213***	***0.0001***
25-Jul								***0.0001***	***0.0002***	***0.0007***
10-Aug									***0.0001***	***0.0001***
25-Aug										***0.0001***
10-Sep										

T. tabaci population was observed both inside and outside greenhouse (Figure 9). Thrips abundance increased from June onwards. Hotspots were detected first (late April) in the greenhouse then (July and September) from the greenhouse to the contiguous orchard (Table 52; Figure 9). Intraspecific associations were significant in late June and from the end of July onwards (Table 54).

Table 54 – Results of association test (Perry & Dixon, 2002) of *T. tabaci* populations in greenhouse GH3 during 2013.

		T. tabaci									
	date	25-Apr	10-May	25-May	10-Jun	25-Jun	10-Jul	25-Jul	10-Aug	25-Aug	10-Sep
		P	*P*	*P*	*P*	*P*	*P*	*P*	*P*	*P*	*P*
T. tabaci	10-Apr	0.9812	***0.0002***	0.9008	0.9985	0.0824	***0.0001***	0.0626	0.5615	0.0833	0.9984
	25-Apr		0.9932	0.9486	***0.0058***	0.2583	0.9963	0.9979	0.6169	0.9946	0.645
	10-May			0.8406	0.7073	0.542	***0.0001***	0.7313	0.9744	0.4746	0.7657
	25-May				0.9052	0.4097	0.6906	0.9569	0.9991	0.9952	0.9965
	10-Jun					0.6965	0.8345	0.9614	0.5078	0.9102	0.3159
	25-Jun						***0.003***	0.4968	0.9397	0.3174	0.9351
	10-Jul							0.0498	0.9601	0.0303	0.9622
	25-Jul								***0.0057***	***0.0015***	***0.0141***
	10-Aug									***0.0241***	***0.0075***
	25-Aug										***0.0019***
	10-Sep										

Captures of predatory thrips were low in spring. They became significant in July when Aeolothripids were aggregated in the southern side of the greenhouse (Table 51; Figure 9). Similarity in the distribution of thrips populations over time was noticed from late June to early July (Table 54).

Table 55 - Results of association test (Perry & Dixon, 2002) of *Aeolothrips* spp. populations in greenhouse GH3 during 2013.

Aeolothrips spp.

Aeolothripss spp. date	10-Jun P	25-Jun P	10-Jul P	25-Jul P	10-Aug P	25-Aug P	10-Sep P
10-May	***0.001***	0.892	***0.0059***	0.551	0.0388	***0.0007***	0.999
10-Jun		0.4362	***0.003***	0.1303	0.1069	0.4213	0.0675
25-Jun			***0.0001***	0.2132	0.097	***0.007***	***0.0001***
10-Jul				0.3081	***0.0139***	***0.0007***	***0.0196***
25-Jul					0.2253	0.1132	***0.0114***
10-Aug						0.2165	0.1962
25-Aug							0.2334
10-Sep							

Orius spp. colonized the greenhouse in late summer but were commonly found in its surroundings. Populations were aggregated in late June in correspondence of the hedgerow and in late August in the fruit orchard (Table 52; Figure 9). Intraspecific association among populations was significant in spring and summer (Table 56).

Table 56 - Results of association test (Perry & Dixon, 2002) of *Orius* spp. populations in greenhouse GH3 during 2013.

Orius spp.

Orius spp. date	10-May P	25-Jun P	10-Aug P	25-Aug P	10-Sep P
10-Apr	***0.0001***	0.6115	0.6496	0.9999	0.9999
10-May		***0.0018***	***0.0048***	0.9999	0.9999
25-Jun			***0.0001***	***0.0128***	0.1759
10-Aug				***0.0001***	0.4818
25-Aug					***0.0001***
10-Sep					

Table 57 - Results of interspecific association test (Perry & Dixon, 2002) between *F. occidentalis* and *T. tabaci* populations in GH3 during 2013. Grey cells indicate association test performed on spatial patterns observed in the same date.

		T. tabaci									
	date	10-Apr	25-Apr	10-May	25-May	10-Jun	25-Jun	10-Jul	25-Jul	10-Aug	25-Aug	10-Sep
F. occidentalis (♀♀)	10-Apr	0.9998	***0.0001***	0.8208	0.6945	***0.0002***	0.3776	0.9982	0.9999	0.8747	0.9988	0.5574
	25-Apr	0.9999	0.0713	0.8774	0.1705	***0.0001***	0.6842	0.9999	0.986	0.4715	0.8525	0.148
	10-May	0.9998	0.5672	0.5998	***0.0001***	0.0981	0.4744	0.9576	0.9996	0.9977	0.9535	0.8906
	25-Apr	0.9999	0.3355	0.8395	***0.013***	0.1413	0.3524	0.9883	0.9554	0.933	0.4884	0.3763
	10-Jun	0.9999	0.0697	0.6995	0.3138	***0.0001***	0.5616	0.9987	0.9035	0.6289	0.8387	0.3766
	25-Jun	0.9999	0.642	0.9435	0.0872	0.0733	0.5158	0.9996	0.6145	0.7533	0.708	0.0595
	10-Jul	0.9999	0.3929	0.9384	***0.0006***	0.0521	0.8703	0.9999	0.9741	0.3974	0.8838	0.3513
	25-Jul	0.9856	0.9885	0.9623	0.4515	0.5632	0.9414	0.9972	0.0565	0.0388	0.0274	***0.0014***
	10-Aug	0.9999	0.9969	0.9878	0.4983	0.2947	0.873	0.993	0.1136	***0.0207***	***0.009***	***0.0001***
	25-Aug	0.9961	0.7953	0.9958	0.9004	0.167	0.6035	0.9497	0.0397	***0.0001***	***0.0149***	***0.0149***
	10-Sep	0.9999	0.6542	0.9991	0.2972	**0.0074**	0.9936	0.9999	0.1958	***0.0178***	0.5126	***0.0005***

Table 58 - Results of interspecific association test (Perry & Dixon, 2002) between *F. occidentalis* and *Orius* spp. populations in GH3 during 2013. Grey cells indicate association test performed on spatial patterns observed in the same date.

		Orius spp.					
	date	10-Apr *P*	10-May *P*	25-Jun *P*	10-Aug *P*	25-Aug *P*	10-Sep *P*
F. occidentalis (♀♀)	10-Apr	***0.0001***	***0.0001***	0.7231	0.9906	0.9999	0.9999
	25-Apr	***0.0036***	0.2634	0.9999	0.9999	0.9999	0.9397
	10-May	0.4577	0.8602	0.9998	0.9999	0.999	0.9373
	25-May	0.2871	0.8531	0.9999	0.9999	0.998	0.9806
	10-Jun	0.0052	0.1382	0.9999	0.9999	0.9999	0.985
	25-Jun	0.399	0.9685	0.9999	0.9999	0.9883	0.6178
	10-Jul	0.1698	0.8741	0.9999	0.9999	0.9997	0.5387
	25-Jul	0.4695	0.9922	0.9999	0.9997	0.7113	0.1146
	10-Aug	0.3531	0.9979	0.9999	0.9999	0.9186	0.612
	25-Aug	0.3359	0.952	0.9997	0.978	0.7526	0.2661
	10-Sep	0.0544	0.7343	0.9999	0.9999	0.998	0.1755

Table 59 - Results of interspecific association test (Perry & Dixon, 2002) between *T. tabaci* and *Aeolothrips* spp. populations in GH3 during 2013. Grey cells indicate association test performed on spatial patterns observed in the same date.

Aeolothrips spp.

T. tabaci date	10-May *P*	10-Jun *P*	25-Jun *P*	10-Jul *P*	25-Jul *P*	10-Aug *P*	25-Aug *P*	10-Sep *P*
10-Apr	***0.0001***	***0.0081***	***0.0012***	***0.0001***	0.0314	***0.0178***	***0.0001***	0.0875
25-Apr	***0.0004***	0.1281	0.9999	0.9967	0.9956	0.4344	0.9435	0.9999
10-May	***0.0137***	0.6038	0.0268	***0.0012***	0.0942	0.0759	***0.0017***	0.1633
25-May	0.9735	0.1743	0.0728	0.6253	0.5491	0.9734	0.983	0.0064
10-Jun	0.5814	0.2808	0.9956	0.8721	0.6879	0.8349	0.9426	0.988
25-Jun	0.1191	0.0611	0.0258	***0.015***	0.3883	***0.0032***	0.5251	0.6394
10-Jul	0.0007	0.1733	***0.0002***	***0.0001***	0.0627	***0.0074***	***0.0002***	***0.0189***
25-Jul	0.9565	0.6389	0.0501	0.0801	0.039	0.1382	0.2631	0.0456
10-Aug	0.9498	0.3465	0.7923	0.9092	0.2413	0.0549	0.7547	0.4084
25-Aug	0.9854	0.9913	***0.0028***	0.0769	0.1327	0.0435	***0.0241***	0.1965
10-Sep	0.9998	0.9502	0.8254	0.9845	0.8392	0.2076	0.7922	0.1684

Table 60 - Results of interspecific association test (Perry & Dixon, 2002) between *T. tabaci* and *Orius* spp. populations in GH3 during 2013. Grey cells indicate association test performed on spatial patterns observed in the same date.

Orius spp.

T. tabaci date	10-Apr *P*	10-May *P*	25-Jun *P*	10-Aug *P*	25-Aug *P*	10-Sep *P*
10-Apr	0.9999	0.9043	**0.0001**	**0.0001**	**0.0001**	0.0949
25-Apr	**0.0001**	0.0001	0.082	0.1045	0.9999	0.9999
10-May	0.9995	0.9815	***0.0179***	0.028	**0.0001**	0.3751
25-May	0.9712	0.9936	0.9368	0.9999	0.7706	0.0129
10-Jun	***0.0055***	***0.0122***	0.9811	0.8653	0.9994	0.9929
25-Jun	0.5414	0.6628	0.1476	0.4055	0.4502	0.9552
10-Jul	0.9999	0.9997	0.0002	***0.003***	**0.0001**	0.1421
25-Jul	0.9814	0.9601	0.5389	***0.0133***	**0.0012**	**0.0079**
10-Aug	0.0837	0.2139	0.605	0.3974	0.6364	0.1113
25-Aug	0.9868	0.9983	0.9408	0.1641	***0.0051***	0.7146
10-Sep	0.0968	0.7536	0.9999	0.3379	0.4339	0.3245

Table 61 - Results of interspecific association test (Perry & Dixon, 2002) between *Orius*

spp. and *Aeolothrips* spp, populations in GH3 during 2013. Grey cells indicate association test performed on spatial patterns observed in the same date.

Orius spp.

Aeolothrips spp. date	10-Apr *P*	10-May *P*	25-Jun *P*	10-Aug *P*	25-Aug *P*	10-Sep *P*
10-May	0,1894	**0,0001**	**0,0001**	**0,0001**	0,2796	0,9486
10-Jun	0,4043	0,2031	**0,0085**	0,2079	0,5271	0,076
25-Jun	0,9999	0,9999	0,6226	0,552	**0,0001**	0,0383
10-Jul	0,9999	0,9997	**0,0078**	**0,0195**	**0,0001**	0,2223
25-Jul	0,9977	0,9268	0,147	0,0693	**0,0133**	0,0277
10-Aug	0,7832	0,5058	**0,02**	**0,0164**	0,0513	0,4234
25-Aug	0,9999	0,8831	**0,0006**	**0,0001**	**0,0001**	0,269
10-Sep	0,9999	0,9999	0,8698	0,8856	**0,0001**	**0,0001**

F. occidentalis and *T. tabaci* populations were associated in spring in various sampling dates and in most cases inside greenhouse (Table 57). *F. occidentalis* was also associated with *Orius* spp. in spring (Table 58) but not with predatory thrips. *T. tabaci* was positively associated with *Aeolothrips* spp. inside greenhouse (Table 59) and with *Orius* spp. in the fruit orchard (Table 60). Additional association involved predatory thrips and predatory bugs (Table 61).

In the open field nursery a low number of *F. occidentalis* females were captured in the hedgerow in spring. Then thrips colonized the open field nursery reaching relatively high populations in June and July (Figure 10). Populations were aggregated in late June, early August and early September with hotspots occurring in nursery areas close to other rose plots (Table 61; Figure 10). Similarities between population distribution over time were found in late July and early August (Table 62).

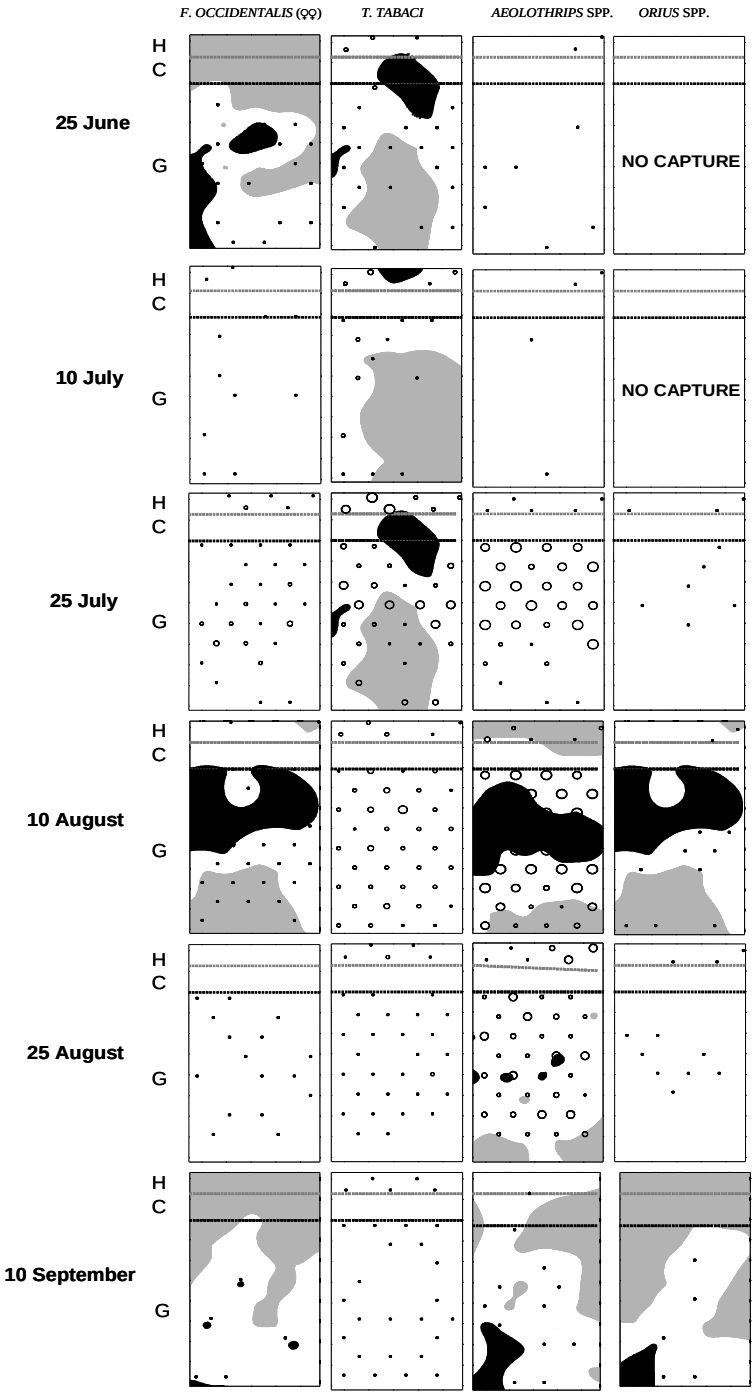

Figure 10 - Spatial patterns of *F. occidentalis*, *T. tabaci*, *Aeolothrips* spp., *Orius* spp. populations in the greenhouse OFN on selected sampling dates during 2013. Black areas correspond to patch ($v_i > 1.5$) whilst grey correspond to gap ($v_j < - 1.5$). Letters 'H', 'C', 'G' indicate 'hedgerow', 'corridor', and 'greenhouse' respectively. Points inside or outside greenhouse correspond to locations of traps with insect captures.

Table 62 - Aggregation index (I) and associated probability (p) of *F. occidentalis*, *T. tabaci*, *Aeolothrips* spp. and *Orius* spp. populations in greenhouse OFN and its surroundings during 2013.

OFN

date	*F. occidentalis* (♀♀)		*T. tabaci*		*Aeolothrips* spp.		*Orius* spp.	
	I	**P**	**I**	**P**	**I**	**P**	**I**	**P**
10-apr	-	-	-	-	-	-	-	-
25-apr	-	-	-	-	-	-	-	-
10-May	-	-	-	-	-	-	-	-
25-May	-	-	0.724	0.7965	-	-	-	-
10-June	1.238	0.3325	1.212	0.2436	1.698	0.121	-	-
25-June	***2.153***	***0.0008***	***1.653***	***0.0072***	1.131	0.2011	-	-
10-July	0.841	0.7468	***1.863***	***0.0032***	1.058	0.3005	-	-
25-July	1.13	0.2011	***2.031***	***0.0008***	***1.785***	***0.0032***	1.333	0.0593
10-Aug	***1.443***	***0.0401***	1.158	0.1843	***1.779***	***0.0056***	0.901	0.6266
25-Aug	0.907	0.6322	1.358	0.0601	***1.438***	***0.0353***	1.251	0.1034
10-Sept	***1.517***	***0.0192***	1.362	0.0577	***1.582***	***0.0144***	***1.817***	***0.0024***

Table 63 - Results of association test (Perry & Dixon, 2002) of *F. occidentalis* populations in greenhouse OFN during 2013.

F. occidentalis (♀♀)

F. occidentalis (♀♀) date	**25-Jun** *P*	**10-Jul** *P*	**25-Jul** *P*	**10-Aug** *P*	**25-Aug** *P*	**10-Sep** *P*
10-Jun	0.3476	-	0.4652	-	-	-
25-Jun		0.4926	***0.0127***	0.2098	0.7117	***0.0002***
10-Jul			0.726	0.2374	0.9028	0.2605
25-Jul				***0.0028***	0.6788	0.1263
10-Aug					0.1201	***0.0167***
25-Aug						0.5035
10-Sep						

T. tabaci was found first in the hedgerow, then also in the nursery (Figure 10). High captures were detected from June to August. Thrips population distribution was found to be aggregated from late June to late July (Table 62) with hotspots involving both the nursery

and the hedgerow (Figure 10). Similarity in the distribution of *T. tabaci* populations over the time was observed in early and mid-summer (Table 63).

Tab 64 - Results of association test (Perry & Dixon, 2002) of *T. tabaci* populations in greenhouse OFN during 2013.

		T. tabaci				
	date	**10-Jul**	**25-Jul**	**10-Aug**	**25-Aug**	**10-Sep**
		P	*P*	*P*	*P*	*P*
T. tabaci	**25-Jun**	***0.0047***	***0.005***	0.6184	0.4062	0.3
	10-Jul		0.0681	0.5288	0.3584	0.8367
	25-Jul			0.3371	0.1113	0.8691
	10-Aug				***0.0134***	0.9803
	25-Aug					0.8528
	10-Sep					

Predaceous thrips were observed in the hedgerow in June, then they moved in the nursery (Figure 10). Thrips population reached the highest levels from July to August. Populations showed to be aggregated from late July to early September (Table 62) with most of patches inside the nursery (also in the hedgerow in late August) (Figure 10). Similarity in the distribution of thrips population over the time was registered between July and August (Table 65)

Table 65 – Results of association test (Perry & Dixon, 2002) of *Aeolothrips* spp. populations in greenhouse OFN during 2013.

Aeolothrips spp.	date	10-Jul *P*	25-Jul *P*	10-Aug *P*	25-Aug *P*	10-Sep *P*
	25-Jun	0.1611	0.9505	0.5261	0.5034	0.0582
	10-Jul		0.9963	0.9855	0.84	0.5493
	25-Jul			***0.0003***	0.0309	0.995
	10-Aug				0.0253	0.6681
	25-Aug					0.3039
	10-Sep					

Orius spp. populations were observed in both the nursery and the hedgerow from late July onwards (Figure 10). Aggregative patterns were shown inside the nursery in early September (Table 62). A significant population spatial structure was observed from late July to late August (Table 66) (Figure 10).

F. occidentalis population was found to be positively associated with *T. tabaci* population in early July in the hedgerow (Table 67). *F. occidentalis* was also observed to be positively associated with predatory thrips in early August and early September; this phenomenon occurred inside and outside the nursery (Table 68). Significant overlapping population distributions were observed between *F. occidentalis* and *Orius* spp. populations in the nursery in early September (Table 69). *T. tabaci* was associated with predatory thrips in late July and early August (Table 70), and with anthocorids in early August (Table 71). These associations were found in the nursery. Finally, a positive association was found between the two beneficials (Table 61).

Table 66 – Results of association test (Perry & Dixon, 2002) of *Orius* spp. populations in greenhouse OFN during 2013.

Orius spp.	*Orius* spp.		
date	**10-Aug**	**25-Aug**	**10-Sep**
25-Jul	***0.001***	***0.0043***	0.8289
10-Aug		***0.0191***	0.8554
25-Aug			0.8995

Table 67 - Results of interspecific association test (Perry & Dixon, 2002) between *F. occidentalis* and *T. tabaci* populations in OFN during 2013. Grey cells indicate association test performed on spatial patterns observed in the same date.

F. occidentalis (♀♀)	*T. tabaci*					
date	**25-Jun** ***P***	**10-Jul** ***P***	**25-Jul** ***P***	**10-Aug** ***P***	**25-Aug** ***P***	**10-Sep** ***P***
25-Jun	0.676	0.8057	0.9011	0.7362	0.9962	0.1757
10-Jul	***0.0066***	***0.0018***	0.1163	0.9387	0.7569	0.3222
25-Jul	0.8935	0.9951	0.5313	0.5138	0.8848	0.799
10-Aug	0.2034	0.2437	0.2517	0.3393	0.865	0.9912
25-Aug	0.4496	0.4441	0.3464	0.0388	0.2253	0.9956
10-Sep	0.8728	0.6285	0.9432	0.6344	0.999	0.369

Table 68 - Results of interspecific association test (Perry & Dixon, 2002) between *F. occidentalis* and *Aeolothrips* spp. populations in OFN during 2013. Grey cells indicate association test performed on spatial patterns observed in the same date.

F. occidentalis (♀♀) \ *Aeolothrips* spp.	10-Jun *P*	25-Jun *P*	10-Jul *P*	25-Jul *P*	10-Aug *P*	25-Aug *P*	10-Sep *P*
10-Jun	-	-	-	0.2196	-	-	-
25-Jun	-	0.0486	0.8846	0.6315	-	-	-
10-Jul	-	0.8546	0.9649	0.2602	-	-	-
25-Jul	0.4623	***0.0154***	0.9683	0.6452	-	-	-
10-Aug	-	0.0714	0.9998	0.189	***0.0004***	0.0685	0.2161
25-Aug	-	0.9822	0.6012	0.033	***0.0104***	0.1625	0.3131
10-Sep	-	0.0677	0.1993	0.9922	0.1968	0.8997	***0.0182***

Table 69 - Results of interspecific association test (Perry & Dixon, 2002) between *F. occidentalis* and *Orius* spp. populations in OFN during 2013. Grey cells indicate association test performed on spatial patterns observed in the same date.

F. occidentalis (♀♀) \ *Orius* spp.	25-Jul *P*	10-Aug *P*	25-Aug *P*	10-Sep *P*
25-Jun	0.9597	0.4416	0.6932	**0.0138**
10-Jul	0.3136	0.9253	0.4409	0.5539
25-Jul	0.8524	0.4567	0.093	0.0704
10-Aug	0.0335	0.0308	0.0608	0.142
25-Aug	0.0502	0.0803	0.6833	0.1486
10-Sep	0.9283	0.4835	0.9345	***0.0087***

Table 70 - Results of interspecific association test (Perry & Dixon, 2002) between *T. tabaci* and *Aeolothrips* spp. populations in OFN during 2013. Grey cells indicate association test performed on spatial patterns observed in the same date.

		Aeolothrips spp.					
	date	**25-Jun**	**10-Jul**	**25-Jul**	**10-Aug**	**25-Aug**	**10-Sep**
		P	*P*	*P*	*P*	*P*	*P*
T. tabaci	**25-Jun**	0.9194	0.9929	***0.0045***	0.1806	0.6448	0.8438
	10-Jul	0.5927	0.385	0.1321	***0.0219***	0.2654	0.4213
	25-Jul	0.8577	0.8555	***0.0035***	0.1507	0.2863	0.9623
	10-Aug	0.708	0.8141	***0.0055***	***0.0019***	0.0835	0.8587
	25-Aug	0.9714	0.8067	***0.0106***	0.054	0.3732	0.9713
	10-Sep	0.5046	***0.0215***	0.996	0.996	0.987	0.1919

Table 71 - Results of interspecific association test (Perry & Dixon, 2002) between *T. tabaci* and *Orius* spp. populations in OFN during 2013. Grey cells indicate association test performed on spatial patterns observed in the same date.

		Orius spp.			
	date	**25-Jul**	**10-Aug**	**25-Aug**	**10-Sep**
		P	*P*	*P*	*P*
T. tabaci	**25-Jun**	0.1095	0.4621	0.8536	0.9367
	10-Jul	***0.0008***	0.1061	0.3408	0.8364
	25-Jul	0.0697	***0.0165***	0.2465	0.9421
	10-Aug	***0.0061***	***0.0178***	0.1466	0.9202
	25-Aug	0.0738	0.0755	0.2276	0.9714
	10-Sep	0.9719	0.9921	0.981	0.7204

Table 72 - Results of interspecific association test (Perry & Dixon, 2002) between *Aeolothrips* spp. and *Orius* spp. populations in OFN during 2013. Grey cells indicate association test performed on spatial patterns observed in the same date.

		Orius spp.			
	date	**25-Jul** ***P***	**10-Aug** ***P***	**25-Aug** ***P***	**10-Sep** ***P***
Aeolothrips spp.	**25-Jun**	0.5649	0.6697	0.2435	***0.01***
	10-Jul	0.7641	0.8671	0.9909	0.5891
	25-Jul	**0.0247**	**0.0162**	***0.029***	0.9999
	10-Aug	**0.0003**	**0.0001**	-	-
	25-Aug	**0.0023**	-	**0.0052**	0.8463
	10-Sep	0.7463	0.6189	0.3919	**0.0014**

Discussion

This study focused on the spatial and temporal dynamics of phytophagous thrips and their predators in a number of sites devoted to the cultivation of ornamentals in a farm located in northern Italy. The selection of sites was based on their level of interaction with external environment: the first greenhouse was opened only at the roof in warmer days, the second on one side, the third on three sides and the last site was an open field nursery. Selected sites were surrounded by hedgerows and cultivated plots. Their potential support in enhancing arthropod exchanges, in particular the colonization by pests and their natural enemies was evaluated.

Monitoring focused on adult stages of phytophagous thrips and their antagonists captured on traps, and thus information on population structure is lacking. Nevertheless, adults were the most appropriate life stages to highlight potential arthropod exchanges between cultivated areas and their surroundings. This approach provided an interesting picture of insect population dynamics in space and time.

F. occidentalis was detected more continuously in the greenhouses and the nursery than on the hedgerows and outside crops both in 2012 and in 2013. In spring the pest was recorded inside the greenhouses or near the main doors that connected experimental plots with compartments devoted to plant cultivation or logistic services. Outside greenhouses *F. occidentalis* was seldom detected in spring and summer. This common trend showed some variation among the cultivation scenarios.

In the greenhouse GH1, in which lateral openings were not present, *F. occidentalis* was detected indoor from spring to summer, rarely outdoor in summer. Populations [both females and males (data not reported)] were aggregated inside the greenhouse from June to July in 2012 and from June to August in 2013 while gaps were detected in the area facing to the hedgerow. The analysis of intraspecific association highlighted a stable population spatial pattern during summer. These observations suggest that hotspots originated from the contiguous greenhouses (presumably infested by this pest) rather than from outside where captures were low and delayed in comparison to those recorded inside the greenhouse.

This situation was somewhat similar to that observed in the greenhouse GH2, opened on the side facing the hedgerow. *F. occidentalis* was detected inside the greenhouse in spring and summer, less commonly outside in the latter period. In contrast with previous scenario, female populations were never aggregated. Interestingly males were aggregated in May (in both years) in the area close to other greenhouses and gaps occurred in the area facing to the hedgerow. Trends in male spread seem to confirm that thrips colonization originated from the contiguous greenhouses rather than from the outside where the pest was captured in few dates and with low numbers (data not reported). In this cultivation scenario population densities were lower than in the previous one and no associations were observed among *F. occidentalis* populations over the time. Insecticide use cannot explain differences observed in pest densities and distribution patterns between GH1 and GH2 greenhouses. In 2012 (June-August) insecticides were applied six times in GH1 and seven times in GH2. One year later insecticide use was higher in GH1 than in GH2 greenhouses (seven vs. three applications, respectively).

Differences between the two greenhouses could be associated to cultural measures (e.g., cutting, removal of flowers), plant transfer, the predominance of flowering plants, and pesticide use. The occurrence of natural enemies of thrips could represent an additional

factor affecting differences between the two greenhouses since a higher presence of predators was observed in GH2. Probably, the incidence of flowering plants represents the main factor in determining the differences between the two greenhouses. During summer an average of 40% in 2012 and 42.2 % in 2013 of plants were flowering in greenhouse GH1, while an average of 10% in 2012 and 17% in 2013 resulted in greenhouse GH2 because of flower removal. Flowers have a key role in *F. occidentalis* adults dispersal. They are oriented to flowers that represent preferable sites for feeding and oviposition (e.g., Yudin et al., 1988; Jacobson, 1997; Kumar, 1995; Rhainds and Shipp, 2003). Consequently the status of host plant can play a role on thrips dispersal: a positive correlation exists between the proportion of senescent inflorescences and the proportion of dispersing females (Rhainds and Shipp, 2003). Studying trap plants, Buitenhuis and Shipp (2006) found that *F. occidentalis* dispersing populations are greatly attracted by flowering plants rather than by plants in vegetative phase. The authors were lead to the conclusion that flowering trap plants can attract and retain the insects that would otherwise move in the greenhouse. *F. occidentalis* tends to disperse in greenhouses with least favoured hosts (Robb, 1989 in Rhainds and Shipp, 2003). Our results confirm the importance of flowers in the dispersal of this thrips species. In GH1, with a higher presence of flowering plants, *F. occidentalis* aggregated as soon as they entered the greenhouse, while in GH2 the low presence of feeding and oviposistion sites (i.e., flowers) induced the dispersal of *F. occidentals* searching for more suitable sites.

The greenhouse GH3 was characterized by three lateral openings: the northern side was partially contiguous to other greenhouses, the western side was adjacent to a hedgerow and the southern side to an orchard. The eastern side (sidewall) was connected with other greenhouses. Hotspots were frequently recorded in the north-eastern corner, inside and outside the greenhouse, close to the main entry. During the season (May-October) of both years, *F. occidentalis* populations were aggregated also in the middle of the greenhouse but rarely in the area facing the hedgerow. Results suggest again that hotspots originated from contiguous greenhouses rather than by the surrounding vegetation. In fact, gaps extended especially from the mid of the greenhouses to the side facing the hedgerow. Intraspecific association was significant for long periods confirming the persistence of thrips and the stability of their population distribution structure in this cultivation scenario. It was highly

infested in both years despite insecticide use (six and nine applications in 2012 and 2013, respectively). Factors affecting the high pressure by *F. occidentalis* populations in this greenhouse need to be identified. Cultivation practices and the dominance of flowering plants for longtime could be major factors involved (see above). Apparently, increasing lateral openings did not reduce the impact of *F. occidentalis* that was likely influenced by the dominance of flowering plant species in this cultivation scenario that reached the highest values (on average 43% and 57.14% in 2013) observed in the greenhouse complex.

Observations in the open field nursery started in June in coincidence with the transfer of targeted plant species, i.e. flowering roses. Therefore, thrips colonization was delayed compared to greenhouses. In 2012, *F. occidentalis* was detected first inside the nursery and its population was much more abundant there than in the hedgerow. Populations showed to be aggregated in June and September in areas contiguous to other rose plots rather than in the proximity of the greenhouse where gaps were frequently observed. Intraspecific association highlighted an unstable population distribution structure. One year later, *F. occidentalis* was more frequent in the hedgerow contiguous to the nursery but thrips population was aggregated again in the opposite area, i.e. close to contiguous rose plots. Population dynamics showed rarely intraspecific association events and did not appear to be affected by insecticide use (five vs. one treatment in 2012 and 2013, respectively).

Data regarding the four cultivation scenarios suggest that the colonization of ornamental plots (in particular protected ornamentals) by *F. occidentalis* is poorly affected by the uncultivated vegetation growing at their margins. Its presence outside ornamental plots was observed with a low frequency and fairly late in the season. This seems to suggest that in some cases ornamental plots could act as infestation sources for outdoor plants. Therefore, handling of infested plants inside greenhouse complexes is likely involved in hotspots detected in non-infested plots. The incidence of flowering plants seems to be a major factor enhancing *F. occidentalis* population increase (e.g., Arzone et *al*., 1989; Higgins, 1992; Gerin et *al*., 1999; de Jager et al., 1993, 1995). Adults can exploit pollen and reproduce actively on this food source (Kirk, 1984, 1985; Trichilo and Leigh, 1988; Kiers et *al*., 2000). Furthermore, flowers can represent a suitable site for meeting/mating (Rosenheim et *al*., 1990; Kiers et al., 2000). Flower colonization especially hidden parts implies a reduction in the impact of pesticides on herbivore thrips (Robb and Parrella, 1989;

Brødsgaard, 1994). Data do not support a significant impact of pesticides on thrips population dynamics. Resistance to many active ingredients have been widely reported (Immaraju et *al*., 1992; Jensen, 2000; Bielza et *al*., 2007) and could explain this phenomenon.

T. tabaci was commonly found in the cultivated plots as well as in their surroundings. Thrips abundance varied in space and time with significant variation among experimental scenarios.

In the greenhouse GH1, *T. tabaci* was detected first inside than outside. In 2012 populations were aggregated more frequently outside (May, July and August) than inside (June). One year later thrips aggregation was observed first outside (July) then in both compartments of this site. Intraspecific association was seldom observed in both years. Data suggest that *T. tabaci* adults can actively spread from uncultivated to cultivated areas and viceversa. The colonization of the greenhouse by this species could be due to cultural practices (e.g., handling and transfer of plants) but the migration from outside is also suggested. In both years population size increased first in the hedgerow and then in the greenhouse despite the application of pesticides. In the greenhouse GH2 *T. tabaci* was detected first inside and then outside in both years. In 2012 captures were higher in the greenhouse than outside and rare aggregation phases involved both compartments in late summer. In 2013 trends inside or outside the greenhouse were less clear and few aggregation phases were recorded. The reduced occurrence of *T. tabaci* seems not to be related to insecticide use that decreased in 2013 compared to 2012. In April of 2012 the occurrence of *T. tabaci* was recorded in the greenhouse GH3 as well as in its surroundings; a first aggregation area extended from the greenhouse to the orchard. Then thrips densities increased more inside the greenhouse than outside with aggregations in various parts of the greenhouse sometimes extended to the orchard. Intraspecific association was significant for long periods as observed for *F. occidentalis.* Therefore, greenhouse GH3 was highly infested by both herbivore thrips but their populations were seldom associated. Trends observed for *T. tabaci* in 2013 were similar: adults were captured inside and outside the greenhouse from spring onwards, and aggregation areas involved the greenhouse area facing to the orchard and this latter. Intraspecific association was significant for long periods. Positive associations between *F. occidentalis* and *T. tabaci* were more frequent

than in 2012. Apparently, both thrips species found favorable conditions in this greenhouse despite the repeated use of pesticides. In June of 2012 *T. tabaci* captures were more abundant in the open field nursery than in the contiguous hedgerow. Later, this species was captured continuously inside and outside the nursery with hotspots located in both compartments of this scenario. In the subsequent year sampling started earlier. *T. tabaci* was captured first in the hedgerow and then inside the nursery. The dynamics of hotspots suggest that adults invaded the nursery coming from the hedgerow. Thrips abundance was not related to differences in insecticide use (five vs. one treatment in 2012 and 2013, respectively). The colonization of open field nursery by natural enemies was observed with a higher frequency compared to other cultivation scenarios (e.g., GH1 and GH2).

Patterns in the colonization of cultivated plots by *T. tabaci* were different from those reported for *F. occidentalis*. The former species was frequently found in the hedgerows and the orchard located at the margins of greenhouses, even in spring. *T. tabaci* adults have been captured in traps located near the roof of all greenhouses involved in this study (data not reported). In particular in GH1 greenhouse, *T. tabaci* was captured from April to July, and from April until August, in 2012 and 2013, respectively; in GH2 greenhouse, adults *T. tabaci* were found on traps from March to September and from May until august, in 2012 and 2013, respectively; finally, in the GH3, thrips captures occurred from May to September, and from April to August, in 2012 and 2013, respectively. The dynamics of hotspots outside and inside cultivation plots and evidence from traps near the roof strongly suggest a role of the natural or cultivated vegetation in *T. tabaci* colonization of contiguous greenhouses. *T. tabaci* is frequently found on cultivated and uncultivated plant outdoor (e.g., Marullo, 2004; Trdan, 2005; Marullo and De Grazia, 2013). *T. tabaci* was found with a higher incidence compared to *F. occidentalis* on traps used to detect wind-borne thrips in Israel (Ben-Yakir and Chen, 2008; Ben-Yakir et al., 2008). Pizzol et al. (2012) investigated thrips diversity on roses under greenhouses and outdoor. Inside greenhouses, *F. occidentalis* was largely dominant over *T. tabaci*, while the proportion between the two species changed outdoor where *T. tabaci* increased. *T. tabaci* can overwinter in temperate climates whereas overwintering of *F. occidentalis* in these conditions is highly limited (e.g., Tommasini and Maini, 1995). Variation in *T. tabaci* abundance among the different cultivation scenarios was also affected by factors reported for *F. occidentalis*, in particular

the incidence of flowering plants. Pesticide use did not exert a clear effect on thrips populations dynamics.

The spatial and temporal distribution of natural enemies of herbivore thrips has been less investigated than that of their prey. Data reported in this paper add original information about the dynamics of predaceous thrips belonging to the genus *Aeolothrips* in protected ornamental crops.

Aeolothripids were detected in the greenhouse GH1 and the contiguous hedgerow in both years. Populations were frequently aggregated outside, never inside the greenhouse. Gaps were located in the side of GH1 facing to other greenhouses. Population distribution structure was not stable over the time. The analysis of interspecific associations revealed interesting patterns in 2012: *F. occidentalis* and *Aeolothrips* spp. were never associated whereas *T. tabaci* and *Aeolothrips* spp. were frequently associated in the hedgerow, especially in late summer. One year later a single association between *F. occidentalis* and aeolothripids was found inside the greenhouse while *T. tabaci* and aeolothripids resulted still associated outside. Therefore, predaceous thrips colonization of this greenhouse appeared to be discontinuous. These predators can disperse by wind and penetrate into close greenhouses when the roof is opened (data not reported). Frequent associations between *T. tabaci* and aeolothripids at the greenhouse margins suggest a role for these antagonists in the natural control of this pest. However, detailed studies are needed to shed light on their impact on thrips populations on wild and cultivated plants.

Aeolothripids were continuously detected inside and outside the greenhouse GH2. Populations reached relatively high densities inside GH2 compared to GH1. In 2012 thrips were aggregated only in the hedgerow while in 2013 aggregation areas extended from the hedgerow to the greenhouse. This phenomenon occurred in August when pesticide use was reduced. The association between predaceous thrips and *T. tabaci* was found in a number of sampling dates and was probably involved in the decline of *T. tabaci* number in mid-summer.

Aeolothripids were detected rarely in the greenhouse GH3 until late June of 2012. Then populations showed to be aggregated inside and outside the greenhouse, especially in proximity of the orchard. In 2013 predaceous thrips captures were lower than those seen in the previous year. In both years predaceous thrips and *T. tabaci* were positively associated

in the greenhouse suggesting interactions between predators and prey.

Predaceous thrips were commonly found in the open field nursery and the contiguous hedgerow and aggregation areas were found in both compartments. In 2012 *Aeolothrips* spp. numbers inside the nursery were high in July when population distribution was positively associated with that of *T. tabaci*. Additional associations were found between aeolothripids and *F. occidentalis* inside the nursery. One year later, predaceous thrips numbers were relatively high in July and August probably favored by prey densities and the lack of insecticide applications. Positive associations with *F. occidentalis* and *T. tabaci* were found inside the nursery; the increase in *Aeolothrips* spp. numbers was apparently related to a decline in thrips densities. Unfortunately, an insecticide was applied in mid-August making difficult to evaluate these effects.

Anthocorids were found in all the cultivation scenarios but with profound differences in terms of abundance and distribution. In 2012 captures were low inside greenhouse GH1 while populations were aggregated in the hedgerow. Gaps were located in the side of GH1 facing to other greenhouses. This situation was similar to that described for aeolothripids. In one case *Orius* spp. were positively associated with *F. occidentalis* inside the greenhouse (May 2012), but typically with *T. tabaci* (or *Aeolothrips* spp.) on the hedgerow. Association between anthocorids and *T. tabaci* at the greenhouse margins suggests the need to investigate more in depth the potential effects of hedgerows and flower strips on functional biodiversity.

In the greenhouse GH2 predatory bug populations were rarely detected in spring. In 2012 this situation changed from late July when aggregations involved the hedgerow and the close plots of the greenhouse. In summer of 2013 aggregation areas were in the hedgerow only. This difference could be associated to the impact of pyrethroids applied in August 2013.

Anthocorids were not frequent inside the greenhouse GH3 while populations showed to be aggregated in proximity of the orchard where their distribution was associated with that of *T. tabaci*. Additional associations were found between *Orius* spp. and *Aeolothrips* especially in the orchard.

Predaceous bugs were commonly recorded in the open field nursery where aggregative patterns were noticed in late summer. *Orius* spp. distribution was associated with that of *F.*

occidentalis, less frequently with *T. tabaci* inside the nursery. Additional associations occurred between *Orius* spp. and *Aeolothrips* spp.

The colonization of greenhouses by anthocorids was less successful than that of predaceous thrips. In most cases the occurrence of *Orius* spp. was limited to hedgerows or the orchard contiguous to the greenhouses. The open field nursery was the most favorable scenario as shown in late summer of 2012. The impact of pesticides is probably the major factors affecting the colonization of greenhouses by anthocorids. However, their penetration into greenhouses seem to be hampered by other factors, probably associated to unfavorable microclimate and probably to anti-lepidopteran nets.

Considering overall data about associations between herbivore thrips and their antagonists we observe four positive association inside GH1, no cases in GH2, nine in GH3 and seventeen in OFN plots. Relatively closed compartments were related to a low incidence of associations. In environments surrounding cultivated plots positive associations were eleven outside GH1, five outside GH2 or GH3 (in the orchard) while no cases were recorded in OFN. The hedgerows contiguous to GH3 and OFN were never involved in associations. Reducing barriers around cultivated plots enhanced the colonization by predators, even if pesticides could alter these dynamics. At the same time, these associations established more frequently outside cultivated plots with the decrease in greenhouse opening.

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Chapter III

Opening greenhouses can affect the occurrence of herbivore thrips and their natural enemies on ornamental crops?

Manuscript in preparation as:

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In this work, I collected most of the data and drafted the manuscript

Abstract

In modern greenhouses interactions with external environment are strongly limited and the occurrence of pests is expected to be reduced. However, this is not true for herbivore thrips. This study was planned to show that opening greenhouse structures is not automatically related to an increase in thrips problems on ornamental crops. were . Observations were performed in four greenhouse complexes devoted to the cultivation of ornamentals. The occurrence of thrips pests *Frankliniella occidentalis* (Pergande) and *Thrips tabaci* Lindelman and their natural enemies (*Aeolothrips* spp. and *Orius* spp.) was compared in semi-closed greenhouses (only roof openings) and open greenhouses (roof and lateral openings). The effect of greenhouse position (inner or outer) inside plots was also studied. *F. occidentalis* seemed to penetrate from the interior of the greenhouse complex and was advantaged by cultivation practices and the connections among greenhouses. *T. tabaci* did not appear to be influenced by lateral openings nor the position in the greenhouse. *T. tabaci* captures on traps placed at the roof suggest a potential role of the greenhouses' surroundings in the colonization of protected crops by this species. Lateral openings promoted the colonization by *Orius* spp. but not by *Aeolothrips* spp. Implications of these results for the promotion of environmentally-sound ornamental productions are discussed.

Introduction

The cultivation of plants under greenhouses was thought to get protection from adverse environmental conditions, pests and diseases and extend the cultivation period (Gullino et al., 1999). Therefore, the use of greenhouses has allowed the cultivation of several ornamental plants outside of their original habitats throughout the World. Greenhouses are designed to provide an ideal environment for plant growth, but on the other hand, can provide optimal conditions for the development of many diseases and arthropods pests (Hussey et al., 1967; Jarvis 1992). A major aim in greenhouses' design is to limit the continuum between external and internal conditions and the development of greenhouse technologies is strongly affected by this purpose. Ventilation, screening, shading, cooling, and heating are developed to manipulate the interactions between internal and external greenhouse environments (Berlinger, 1999). However the conjugation of different needs in

plant growing is a challenge in greenhouse management. The exclusion of arthropods pests, optimal ventilation and lighting inside greenhouses are conflicting aspects that research in screening technologies is attempting to conjugate (e.g., Teitel, 2007; Ben-Yakir et al., 2008; Shipp et al., 2011), but the consequences of the use of insect-proof screens on greenhouse internal climate are still matter of discussion (Fatnassi et al., 2006; Tanny, 2013). Highly equipped, climate-controlled closed or semi-closed greenhouses represent the cutting edge technology in this field (Heuvelink et al., 2008, Vadiee and Martin, 2014). In these greenhouses the interactions with external environment are strongly limited and the occurrence of pests is expected to be reduced (Montero et al., 2008), although a precise evaluation of implications in pest management are lacking.

Spatial component of pests occurrence in greenhouses is an issue with clear consequences on the effects of above mentioned greenhouse technologies on pest management. Among arthropods of economic importance for protected crops, herbivore thrips *Frankliniella occidentalis* (Pergade) and *Thrips tabaci* Lindelman are major worldwide pests (Tommasini and Maini, 1995). The two thrips species can infest cultivated plants in field and greenhouse conditions, and can feed and reproduce on a large number of wild plants (e.g., Tavella et al., 1991; Pearsall and Myers, 2001; Pizzol et al., 2012). Along with direct damage caused by feeding, they are vectors of several viruses (e.g., Wijcamp et al., 1995; Mound, 1996). Therefore, they are considered with major concern on ornamental crops (e.g., Parella and Jones, 1987; Jacobson, 1997; Cloyd, 2009).

Due to their small size, it is generally assumed that dispersal by wind can play an important role in their colonization patterns, with individuals having minimal control on flight paths and destination (Lewis, 1997). However, take-off and settling phases of the dispersal, as well as local flight can be controlled by thrips and responses to colour, UV reflectance, scent and host plant quality have been studied (e.g., Lewis, 1973, 1997; Rhainds and Shipp, 2003, Rhainds et al., 2005; Buitenhuis and Shipp, 2006; Kigathi and Poehling 2012). Within greenhouses, the presence of thrips can be observed in an aggregate dispersion pattern (e.g., Steiner, 1990; Shipp and Zariffa, 1991; Nava et al., 1994; Cho et al., 1998; Wang and Shipp, 2001; Park et al., 2009). Few studies considered the spatial component of thrips distribution in greenhouses suggesting a role of greenhouse margins and entries for the invasion and development of thrips populations inside greenhouses (e.g.,

Rhainds and Shipp, 2004; Poncet et al., 2010).

The promotion of biological control is a key factor in the framework of Integrated Pest Management (IPM) in greenhouses (van Lenteren, 2012). The importance of augmentative biocontrol against thrips is widely recognized, and in warm winter climates natural occurring biocontrol agents can be of particular importance (Riudavets, 1995; Sabelis and Van Rijn, 1997; van Lenteren, 2000). Thrips' natural enemies can occur also in landscapes surrounding greenhouses (Shipp et al., 1992; Tommasini, 2004; Trdan, 2005, Carvalho et al., 2006; Bosco and Tavella, 2008, 2013; Conti, 2009; Atakan 2010; Veres et al., 2011). Successful control of thrips by naturally occurring predatory bugs (i.e., *Orius* spp.) has been observed on sweet peppers under plastic tunnels (Bosco et al., 2008). Naturally occurring *Orius* spp. can aggregate within greenhouses (Shipp et al., 1992), but information on greenhouses openings on their distributions is not available.

Knowledge on the colonisation patterns of greenhouses by pests and their natural enemies requires ad hoc studies (Gabarra et al., 2004). This aspect can be of particular importance since innovation in greenhouse industry are moving toward the reduction of the interactions of internal compartments with external environment. Modern greenhouses are often structured in big complexes where the connections with internal areas, such other greenhouses or logistic areas, are likely to be greater than those with the outdoor environment. The aim of the study was to understand the implication of these factors in the management of thrips pests in ornamental crops.

Materials and Methods

Study system

The occurrence of thrips pests and their natural enemies was compared in greenhouse complexes characterized by semi-closed greenhouses (only roof openings) and open greenhouses (roof and lateral openings). A first comparison involved greenhouse plots with or without lateral openings. In each plot we also evaluated the effect of the position in the greenhouse with respect of the connection with interior compartments, and lateral openings/sidewalls on the abundance of thrips and their natural enemies. In particular, we compared inner areas, located in proximity of the connection with interior compartments

with outer areas, close to lateral openings or sidewalls of the complex.

This study was performed from 2011 to 2013 in four greenhouse complexes devoted to the cultivation of ornamentals. All greenhouse complexes were located in the Veneto region (North-eastern Italy) and shared similar outdoor climate parameters (Mediterranean North environmental zone according to Metzger et *al*., 2005). In all greenhouses, computer controlled roof openings and ventilators were present. Greenhouses considered in this work were rectangular shaped and with glass used as covering materials at the roof and polycarbonate sidewalls. Within each complex a number of independent plots were identified and classified as "with lateral openings" if lateral openings were present on more than 25% of their perimeter, or "without lateral openings" if no openings on their perimeter occurred. Five "with lateral openings" plots and five "without lateral openings" plots were identified. At the end of June 2012, one plot without lateral opening was opened on one side and thus it changed its category. Openings were regulated using computer controlled systems, from late spring until autumn in order to maintain an indoor temperature of 25°C. In all greenhouses common cultivation practices were adopted and fungicides and insecticides were applied when needed to control major pests and diseases.

Observations were performed from June to September in 2011, from April to August in 2012, and from April to July in 2013. During observation periods the same ornamental plants (e.g., *Pelargonium* spp., *Cyclamen* spp., *Rosa* spp., *Impatiens* spp., *Primula* spp.) were cultivated in the different plots. Data on insect abundance were obtained using 15 x 15 cm light yellow and blue glue sticky traps fastened to small plastic stakes. Within each plot a group of 3-4 traps were placed every 5-10 m in the inner and outer areas distant 25-50 m. Traps were placed every 15 days initially in the plant canopy and raised up during plants growth; they were collected after a week, covered with plastic wrap and transferred to the laboratory where insects were identified and counted under a dissecting microscope. *Frankliniella occidentalis* and *T. tabaci* were identified following the descriptions reported in Moritz et *al*. (2004) and Marullo (1993). Among natural enemies, predatory thrips and Anthocoridae were the most abundant and their identification was performed at genus level following Péricart (1972) and Mound and Kibby (1998).

Data analysis

Data on herbivore thrips and predatory insects captured on traps during the three years were separately analysed using a Restricted Maximum Likelihood (REML) repeated measures model with the Proc MIXED of SAS (SAS Institute Inc., 1999). In this analysis lateral openings, position in the greenhouse, year, time of sampling nested within year and their interactions were considered as source of variation for *F. occidentalis*, *T. tabaci* and predatory insects captures. F test was used to evaluate their effects ($\alpha = 0.05$). Groups of traps positioned in the same plots and position into greenhouses were considered as replicates in the analysis. In the model, "greenhouse complex" and "plots" were considered as random effect terms. Degrees of freedom were estimated using the Kenward–Roger method (Littell et al., 1996). According to Aikaike's Information Criterion, first-order autoregressive proved to be the best fitting covariance structure for correlating different sampling dates made on the same plot (Littell et al., 1996). Differences among treatments were evaluated with a t-test ($\alpha = 0.05$) to least square means. The SLICE option of the LSMEANS statement was used to partition effects variation during observation periods (SAS Institute Inc., 1999). All data were checked for normality assumption and thus the numbers of insects per traps were square root transformed.

Results

Herbivore thrips

Frankliniella occidentalis adults were continuously captured during the observation period and this species was dominant among herbivore thrips in the greenhouses (Figures 1, 2). *F. occidentalis* captures were influenced by the position in the greenhouse resulting higher in the inner part (Table 1, Figure 1). The abundance of *F. occidentalis* adults varied among time within year with differences between greenhouses with lateral openings (2011: $F_{7, 310} = 1.78$; $P = 0.091$; 2012: $F_{9, 304} = 4.62$; $P < 0.001$; 2013: $F_{7, 314} = 4.46$; $P < 0.001$; Figure 1), and greenhouses without lateral openings (2011: $F_{7, 310} = 2.04$; $P = 0.051$; 2012: $F_{9, 187} = 1.85$; $P = 0.058$; 2013: $F_{7, 183} = 10.04$; $P < 0.001$; Figure 1).

Thrips tabaci was also captured in the greenhouses during the three years (Figure 2), but no effects of position in the greenhouse nor of lateral openings were found (Table 1). The

number of *T. tabaci* varied among years, with higher captures in 2012 than 2011 ($t_{92.2}$ = 2.86; P = 0.005; Figure 2) and 2013 (t_{105} = 5.18; P < 0.001; Figure 2), and in 2011 compare to 2013 (t_{101} = 2.33; P = 0.0217; Figure 2). The number of captures varied in time within years (Table 1). A variation in time of population densities was observed in the three years where lateral openings were present (2011: $F_{7, 339}$ = 2.47; P = 0.017; 2012: $F_{9, 334}$ = 5.55; P < 0.001; 2013: $F_{7, 332}$= 3.53; P = 0.001; Figure 2), while only in 2012 where lateral openings were absent (2011: $F_{7, 337}$ = 1.09; P = 0.367; 2012: $F_{9, 336}$ = 4.37; P < 0.001; 2013: $F_{7, 335}$= 0.79; P = 0.598; Figure 2).

Table 1 - Results of Restricted Maximum Likelihood repeated measures analysis with number of herbivore thrips captured on traps as dependent variables. Degrees of freedom in all models were calculated using the Kenward-Roger method.

Sources of variation	F	d.f.			P
Frankliniella occidentalis					
Lateral openings	0.89	1	;	32.0	0.352
Position in the greenhouse	16.25	1	;	121.0	< 0.001
Year	0.31	2	;	59.5	0.734
Time (Year)	5.86	23	;	334.0	< 0.001
Lateral openings * Position in the greenhouse	0.41	1	;	123.0	0.524
Year * Lateral openings	1.99	2	;	126.0	0.142
Time (Year) * Lateral openings	3.26	23	;	350.0	< 0.001
Year * Position in the greenhouse	1.42	2	;	127.0	0.247
Time (Year) * Position in the greenhouse	0.41	23	;	349.0	0.994
Year * Lateral openings * Position in the greenhouse	0.72	2	;	129.0	0.491
Time (Year) * Lateral openings * Position in the greenhouse	0.73	23	;	349.0	0.812
Thrips tabaci					
Lateral openings	1.94	1	;	47.5	0.170
Position in the greenhouse	0.43	1	;	82.8	0.512
Year	13.77	2	;	98.9	< 0.001
Time (Year)	4.24	23	;	347.0	< 0.001
Lateral openings * Position in the greenhouse	0.23	1	;	86.8	0.629
Year * Lateral openings	1.77	2	;	102.0	0.175
Time (Year) * Lateral openings	1.77	23	;	346.0	0.017
Year * Position in the greenhouse	0.13	2	;	97.1	0.875
Time (Year) * Position in the greenhouse	1.12	23	;	347.0	0.324
Year * Lateral openings * Position in the greenhouse	0.27	2	;	102.0	0.765
Time (Year) * Lateral openings * Position in the greenhouse	0.45	23	;	346.0	0.988

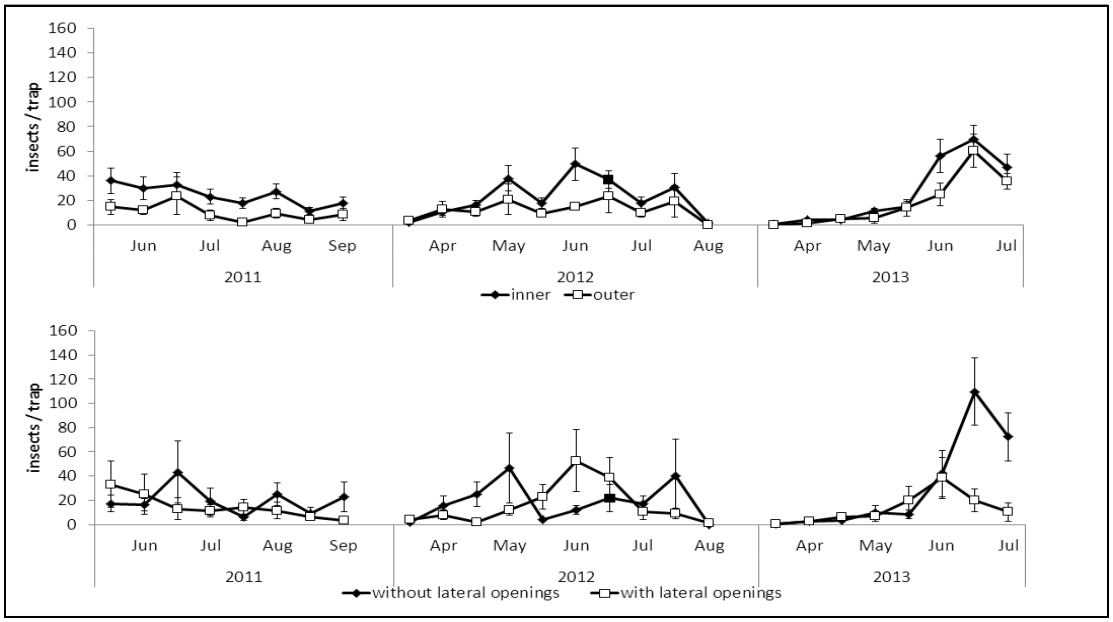

Figure 1 - Number (mean ± std. err.) of *Frankliniella occidentalis* adults captured on sticky traps from 2011 to 2013 in plots characterized by different positions in the greenhouse and by the presence/absence of lateral openings.

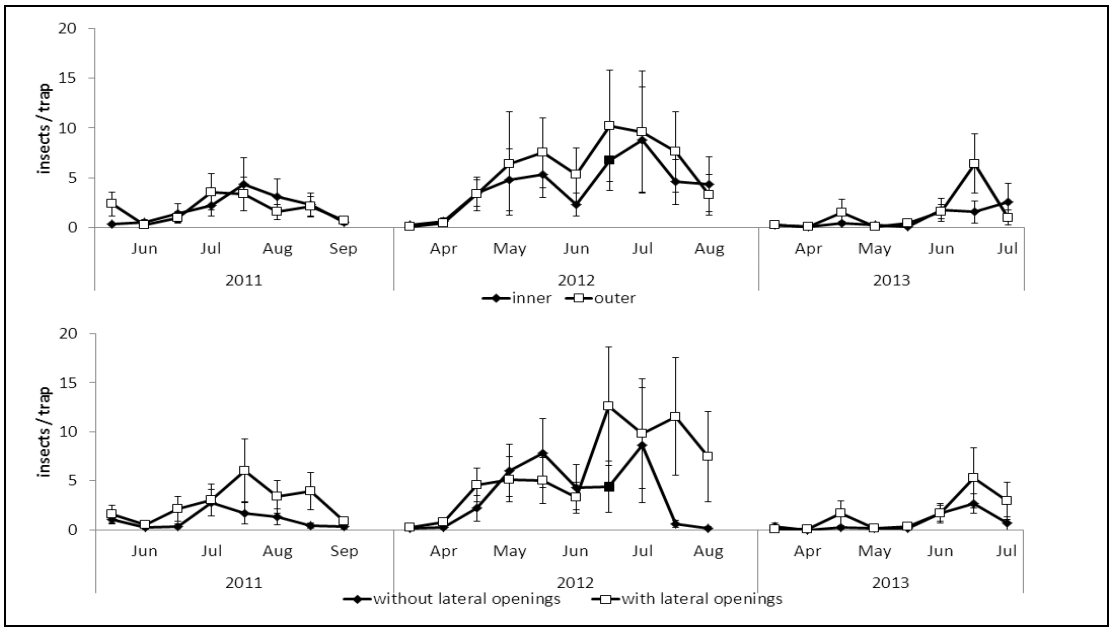

Figure 2 - Number (mean ± std. err.) of *Thrips tabaci* adults captured on sticky traps from 2011 to 2013 in plots characterized by different positions in the greenhouse and by the presence/absence of lateral openings.

Predatory insects

Among predatory insects, those belonging to the genera *Aeolothrips* spp. and *Orius* spp. were frequently recorded (Figures 3, 4). The number of *Aeolothrips* spp. was not influenced by the presence of lateral openings and the position in the greenhouse (Table 2, Figure 4). Captures varied among years (Table 2, Figure 3). A higher number of predatory thrips was captured in 2011 than 2012 ($t_{42.5} = 5.31$; $P < 0.001$; Figure 3) and 2013 ($t_{31.4} = 3.39$; $P = 0.002$; Figure 3), while no differences emerged between captures in 2012 and 2013 ($t_{126} = 1.43$; $P = 0.156$; Figure 3). A variation in captures was observed in time within years (Table 2, Figure 3), but this was observed in two out of three years in greenhouses with lateral openings (2011: $F_{7, 327} = 12.79$; $P < 0.001$; 2012: $F_{9, 327} = 2.39$; $P = 0.012$; 2013: $F_{7, 313} = 2.65$; $P = 0.011$; Figure 3), while only in the first year in greenhouses without lateral openings (2011: $F_{7, 325} = 9.06$; $P < 0.001$; 2012: $F_{9, 320} = 0.63$; $P = 0.769$; 2013: $F_{7, 320} = 1.51$; $P = 0.163$; Figure 3).

Orius spp. densities were higher where the greenhouses were laterally opened (Table 2; Figure 4). Their numbers varied among years and time within year (Table 2). A higher number of *Orius* spp. was captured in 2011 than 2012 ($t_{204} = 3.84$; $P < 0.001$; Figure 4) and 2013 ($t_{152} = 5.10$; $P < 0.001$; Figure 4), while no differences emerged between captures in 2012 and 2013 ($t_{201} = 1.70$; $P = 0.089$; Figure 4). A significant interaction “Lateral openings * time (year)” was observed: the variation in time within year was significant in the greenhouses with lateral openings ($F_{25, 359} = 6.17$; $P < 0.001$; Figure 4), while was not significant in greenhouses without lateral openings ($F_{25, 360} = 0.77$; $P = 0.783$; Figure 4).

Table 2 - Results of Restricted Maximum Likelihood repeated measures analysis with number of predatory insects captured on traps as the dependent variables. Degrees of freedom in all models were calculated using the Kenward-Roger method.

Source of variations	F	d.f.		P
***Aeolothrips* spp.**				
Lateral openings	0.01	1 ;	22.5	0.968
Position in the greenhouse	1.49	1 ;	92.6	0.226
Year	14.06	2 ;	50.2	<0.001
Time (Year)	6.63	23 ;	337.0	<0.001
Lateral openings * Position in the greenhouse	2.91	1 ;	94.7	0.091
Year * Lateral openings	0.21	2 ;	99.9	0.810
Time (Year) * Lateral openings	2.49	23 ;	344.0	<0.001
Year * Position in the greenhouse	0.33	2 ;	106.0	0.722
Time (Year) * Position in the greenhouse	0.72	23 ;	344.0	0.823
Year * Lateral openings * Position in the greenhouse	0.32	2 ;	109.0	0.728
Time (Year) * Lateral openings * Position in the greenhouse	0.47	23 ;	343.0	0.982
***Orius* spp.**				
Lateral openings	9.07	1 ;	5.8	0.025
Position in the greenhouse	0.03	1 ;	174.0	0.864
Year	14.38	2 ;	184.0	<0.001
Time (Year)	3.03	23 ;	357.0	<0.001
Lateral openings * Position in the greenhouse	0.43	1 ;	174.0	0.512
Year * Lateral openings	2.66	2 ;	185.0	0.073
Time (Year) * Lateral openings	2.13	23 ;	357.0	0.002

Year * Position in the greenhouse	0.49	2	;	180.0	0.615
Time (Year) * Position in the greenhouse	0.45	23	;	356.0	0.988
Year * Lateral openings * Position in the greenhouse	0.68	2	;	180.0	0.510
Time (Year) * Lateral openings * Position in the greenhouse	0.52	23	;	356.0	0.971

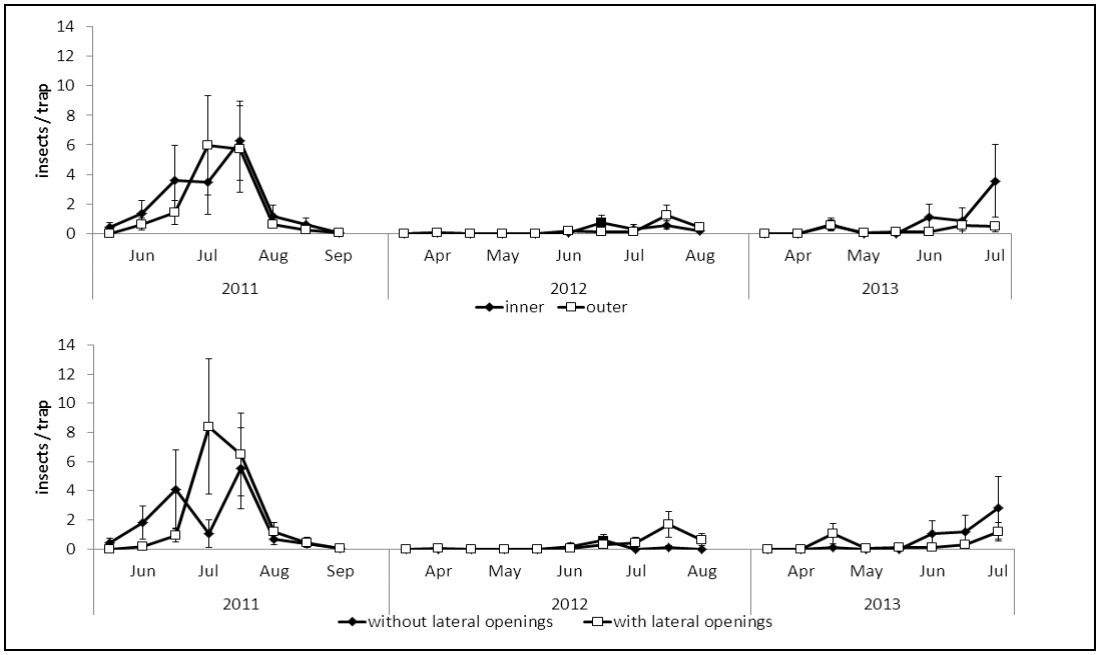

Figure 3 - Number (mean ± std. err.) of *Aeolothrips* spp. adults captured on sticky traps from 2011 to 2013 in plots characterized by different positions in the greenhouse and by the presence/absence of lateral openings.

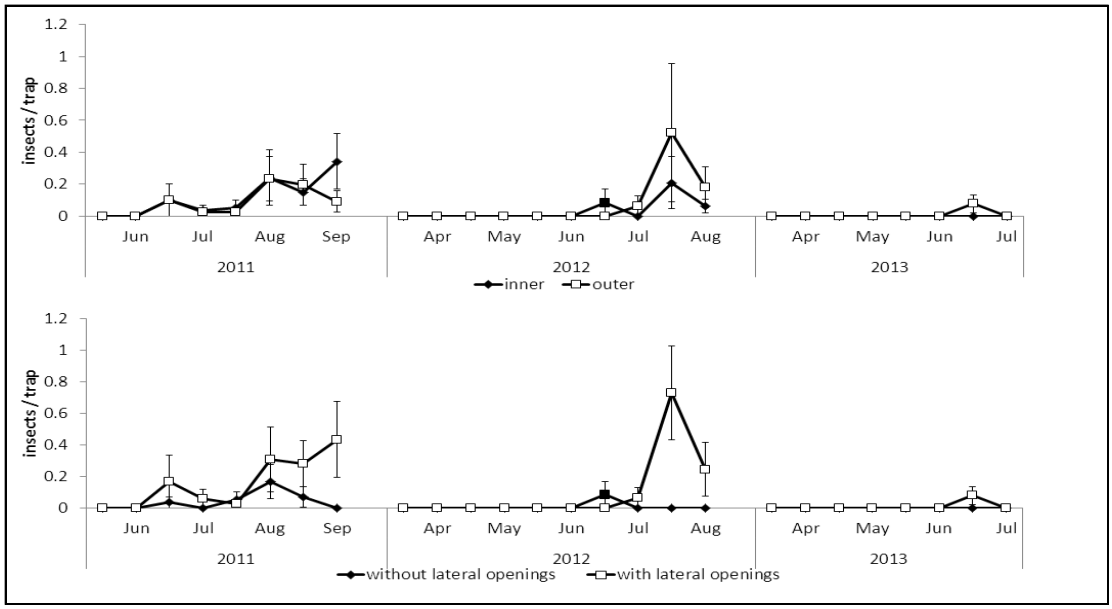

Figure 4 - Number (mean ± std. err.) of *Orius* spp. adults captured on sticky traps from 2011 to 2013 in plots characterized by different positions in the greenhouse and by the presence/absence of lateral openings.

Discussion

Factors here considered caused different effects on the two herbivore thrips species. Results showed an important role of greenhouse connections with interior compartments on the occurrence of *F. occidentalis*, resulting higher in inner plot areas; in contrast, no effects of lateral openings were found on the abundance of this species. The inner and outer parts of plots were similar in terms of climate parameters. *F. occidentalis* is characterized by a low dispersal ability within the greenhouse (Rhainds and Shipp, 2004). The higher number of individuals captured in the inner areas suggests that major inflows in greenhouses are originated from the doors connecting greenhouses to other cultivated plots or logistic and service areas. The latter are used for internal transfer and short –term storage for both in- and outgoing plants and cultivation materials. Moreover doors are used by workers. This confirms previous observations made on protected roses in France (Poncet et al., 2010). *F. occidentalis* can colonize greenhouses from plants moved outside of the plots close to the doors, and for some extent also transportation by workers can also contribute. It is well known that artificial dispersal linked to human activities is the major driver in long distance spread and invasion patterns of this pest (Lewis, 1997; Morse and Hoddle, 2006).

Regarding *T. tabaci* no clear patterns emerged in our study. This thrips did not appear to be influenced by lateral openings nor the position in the greenhouse. It has been found that *T. tabaci* population can first aggregate at the greenhouse margins and then inside (see chapter 1 of this thesis). Some traps were placed close to the roof openings to investigate possible thrips flows from outside. *T. tabaci* was frequently captured on these traps (data not shown), while few captures of *F. occidentalis* were detected.

Results suggest a different greenhouse colonization pattern between the two species. *F. occidentalis* seems to penetrate from the interior of the greenhouse complex advantaged by cultivation practices. *T. tabaci* can come from outdoors and enter the greenhouse through roof opening even if previous factors acting for *F. occidentalis* could be also involved.

Observations carried out in two experimental greenhouse complexes showed that *T. tabaci* is frequent outside greenhouses, while *F. occidentalis* is much more frequent inside (see chapter 1). The two species differ in their origins. *T. tabaci*, native of the Mediterranean area, is established in temperate areas since long time, and is well adapted to outdoor conditions (Mound, 2005; Morse and Hoddle, 2006). *F. occidentalis* is considered endemic to Western North America, from Mexico to Alaska (Bryan and Smith, 1956), its establishment and spread in Europe and elsewhere is considered to be associated to an "insecticide resistant glasshouse" strain that prefers protected environments to outdoor conditions of temperate climates (Tommasini and Maini, 1995; Mound, 1995; Morse and Hoddle, 2006; Kirk and Terry, 2003). Recent research using molecular techniques support the existence of these different cryptic species/ecotypes (so-called "glasshouse" and "lupin") in *F. occidentalis* (Rugman-Jones et al., 2010; Yang et al., 2012). *F. occidentalis* shows extraordinary ecological niche adaptation, and this has been suggested a key-factor determining the invasion by western flower thrips (Brunner and Frey, 2010). These authors hypothesized that the spread of *F. occidentalis* was determined by the adaptation of an ecotype originating from a restricted source area and/or pre-adapted genotypes having an advantage in greenhouse conditions. The adaptation of *F. occidentalis* to greenhouse conditions could also explain the different thrips population levels (average of three years: 18.67 *F. occidentalis*/trap vs. 2.73 *T. tabaci*/trap) found in greenhouses. Pesticide resistance can be another important factor involved in these differences since both thrips species can develop resistance (e.g., Brødsgaard, 1994; Shelton et al., 2003). Moreover, the

glasshouse strain of *F. occidentalis* is characterized by a high resistance to pesticides (Brødsgaard, 1994; Martin and Workman, 1994). According to the Arthropod Pesticide Resistance Database (http://www.pesticideresistance.com), 157 cases (23 active ingredients) of resistance have been reported for *F. occidentalis,* while 76 cases (14 active ingredients) for *T. tabaci*. Pesticide use in the greenhouse is likely to pose selection pressure on the two thrips and the *F. occidentalis* "glasshouse insecticide resistant" strain could be advantaged over *T. tabaci*.

Regarding natural biocontrol agents, an effect of lateral openings was found on *Orius* spp. rather than on *Aelothrips* spp. However, in traps placed close to roof openings predatory thrips were frequently captured with a colonization patterns similar to *T. tabaci* (see also chapter 1). The presence of both predators was not high during the observation period, and their establishment was probably limited by pesticide use. Results suggest that the colonization of greenhouses by naturally occurring predators is enhanced by openings. Outdoor a range of *Orius* spp. species can effectively control thrips (van de Veire and Degheele, 1992; Riudavets, 1995; Tavella et *a*l., 1994, 2000; Bosco et *al*., 2013). Natural occurring anthocorids can perform better on *F. occidentalis* populations than released species (Bosco et *al*., 2008). The potential of predatory thrips as biological control agents is less known (Riuvadets and Castañé, 1998; Trdan et al., 2005), but promising results in *F. occidentalis* control on ornamentals has been recently obtained by *Franklinothrips vespiformis* Crawford augmentative releases (Pizzol et *al*., 2007; Poncet et *al*., 2008; Nammour et *al*., 2008).

Results obtained here have implication for pest management of thrips pest in modern greenhouses. The use of insect-proof screening placed on ventilation openings of the greenhouse is expected to have minimal impact on *F. occidentalis,* the pest of primary importance for greenhouse ornamentals (Cloyd, 2009). Its colonization of greenhouse comes mainly from indoor. Major importance for the control of this thrips is the control of door openings and insects carried passively by workers. Our results indicate that areas around doors are at higher risk of *F. occidentalis* establishment and outbreaks and this should be considered in pest scouting and control measures. Rhainds and Shipp (2004) considering the limited dispersal of *F. occidentalis*, concluded that outbreaks may be effectively suppressed by applying insecticides or releasing natural enemies in relatively

small concentric areas surrounding the edges of greenhouses. We can add to this conclusion that major attention in control measures application should be place to area around connection area with interior compartments.

The use of thrips-proof screening (Teitel, 2007 and citation therein) is likely to have major implication for *T. tabaci*. On the other hand, the use of screens will exclude the occurrence of natural enemies. These aspects should be carefully considered in the context of IPM in ornamental crop systems. In these systems, the zero tolerance for aesthetic injuries has limited the use of biological control in favour of chemical control. However the use of biological control is increasing, mostly because of the occurrence of resistance (van Lenteren and Woets, 1988; van Lenteren, 2000). Modern pest management in ornamentals is now targeted to minimal aesthetic injury using "holistic" approach (Cloyd, 2009). In this scenario the promotion of natural biological control is an important point that should be conjugated with the others cultivation needs in greenhouse design. An interesting approach in this direction is the selective use of insect-proof screens when and where is necessary to prevent immigration of insect pests and promote ventilation, as proposed by Ben-Yakir et al. (2008). The promotion of the greenhouse colonization by natural enemies should be also included in future research on greenhouse design for the promotion of environmentally-sound ornamental productions.

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Chapter IV

Combined use of biological control agents against canopy- and soil-dwelling stages of *Frankliniella occidentalis* on cyclamens

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The Manuscript in preparation as:

Alberto Pozzebon, Andrea Boaria, Carlo Duso - Combined use of biological control agents against canopy- and soil-dwelling stages of *Frankliniella occidentalis* on cyclamens

In this work, I contributed to collect the data and drafted the manuscript.

Abstract

Frankliniella occidentalis is a major pest in agriculture. Problems in its control are mainly due to cryptic behaviour and insecticide resistance exhibited by this pest. The use of Biological Control Agents (BCAs) and biopesticides against thrips pests can represent an alternative to insecticide use. We evaluated the effectiveness of a number of BCAs in the control of *F. occidentalis* populations on cyclamens under semi-field conditions. Three BCAs (*Amblyseius swirskii*, *Neoseiulus californicus* and *Orius laevigatus*) were applied at canopy level and two (*Macrocheles robustulus* and *Steinernema feltiae*) at soil level. We compared the control level obtained by single and combined releases of BCAs at canopy and soil levels in greenhouse conditions using a factorial design experiment. The most effective BCAs at canopy level were the predatory mites while both BCAs used at soil level determined satisfactory control. The combined release of BCAs on the canopy and the soil resulted an effective strategy for biological control of *F. occidentalis* on cyclamens.

Introduction

Frankliniella occidentalis Pergande is one of the most economically important pest of greenhouse ornamentals around the World (Tommasini and Maini, 1995). It causes serious direct damage by feeding to flowers and leaves, leading to a reduction in economic value of various ornamental crops (Lewis, 1997; Cloyd, 2009). It is also of importance as vector of plant viruses: TSWV (Tomato Spotted Wild Virus) but also TSV (Tobacco Streak Virus) and INSV (Impatients Necrotic Spot Virus) can be effectively transmitted to susceptible crops (e.g., Allen and Matteoni, 1988; Reley et al., 2011). *F. occidentalis* acquires viral particles from infected plants as larvae and transmit them as adults (e.g., Ullman et al., 1997; Whitfield et al., 2005).

F. occidentalis is characterized by a cryptic behaviour: first and second instars, and adults are canopy inhabiting stages while pupation occur in soil or in hidden sites within flowers (Tommasini and Maini, 1995; Broadbend et *al*., 2003; Berndt et *al*., 2004). The choice between soil or flowers for pupation depends on relative humidity (pupation occur into soil with RH < 81%) or the availability of hidden sites (Buitenhuis and Shipp, 2008; Steiner et al., 2011; Holmes et *al*., 2012). This behaviour together with insecticide

resistance makes this insect a difficult pest to control (Brødsgaard, 1994; Jensen, 2000; Jacobson et *al*., 2001; Kiers et *al*., 2000). Pesticide resistance has promoted a strong interest for biological control agents (BCAs) and this phenomenon has involved ornamental crops as well (van Lenteren, 2000; Cloyd, 2009). Most of the proposed biocontrol strategies on ornamentals considered the use of BCAs against canopy-dwelling stages (e.g., Glockemann, 1992; Van de Veire and Degheele, 1992; Riudavets, 1995; de Courcy Williams, 2001; Skirvin et al., 2006; Van Driesche et al., 2006). More recently attention has been posed to the control of soil-dwelling stages (e.g., Buitenhuis and Shipp, 2005; Messelink and van Holsten-Saj, 2008; Arthur and Heinz, 2006; Skinner, 2012).

In ornamental crops pest damage is often related to the aesthetic value of these crops (Parella and Jones, 1987; Cloyd, 2009). In this framework it is assumed that more control tools should be applied to provide satisfactory levels of pest control (van Lenteren, 2000). Some studies on the biological control of *F. occidentalis* on ornamentals were performed combining the predatory mites *Neoseiulus cucumeris* (Oudemans) and *Hypoaspis aculeifer* (Canestrini) (e.g., Linnamäki et al., 1998; Wiethoff et al., 2004; Thoeming and Poehling, 2006). More recently, the combined use of wide range of BCAs at the canopy and soil levels has been planned, in particular in Australasia (e.g., Manners et al., 2013).

In this paper we focused on the combined use of BCAs against canopy and soil dwelling life-stages of *F. occidentalis*. We used two predatory mites *Amblyseius swirskii* Athias-Henriot and *N. cucumeris* (Acari: Phytoseiidae) and the predatory bug *Orius laevigatus* (Fieber) (Heteroptera: Anthocoridae) at canopy level, while the predatory mite *Macrocheles robustulus* (Berlese) (Acari: Macrochelidae) and the entomoparasitic nematode *Steinernema feltiae* (Filipjev) (Rhabditida: Steinernematidae) at soil level. Predators used at canopy level are well known *F. occidentalis* antagonists used in augmentative or inundative biocontrol strategies on various crops including ornamentals (e.g., Jacobson et al., 1997; Skirvin et al., 2006; Messelink et al., 2008; Buitenhuis et al., 2014). The entomoparasitic nematode *S. feltiae* can be employed against *F. occidentalis* in ornamental crops through foliar or soil applications, but soil applications are considered most cost/effective (e.g., Ebbsa et al., 2001; Buitenhuis et al., 2005; Arthurs and Heiz, 2006; Trdan et al., 2007). Less studies are available on *M. robustulus* that is a soil inhabiting mite, used against *F. occidentalis* on chrysanthemum (Messelink and van Holsten-Saj, 2008).

This study was performed on potted cyclamens, that are considered optimal crops for the application of biological control due to their long production cycle (de Courcy Williams, 1993). *F. occidentalis* can cause both direct and indirect damage (vectoring virus) to cyclamens (Allen and Matteoni, 1988). We compared the control level obtained by single and combined release of BCAs, at canopy and soil levels in greenhouse conditions using a factorial design experiment.

Materials and Methods

Insects rearing

Thrips rearing was performed according to the method described by DeGraff et al. (2009) with minor changes. Thrips were reared on cucumber leaves held into rectangular boxes (30cm x 15cm x 20cm), supplied weekly with pollen (*Typha latifolia*) and replenished by water for assuring optimal humidity conditions. Rearing units were kept at 25±1 °C, 70% ± 10% of relative humidity, and a photoperiod of 16:8 (L:D). Thrips were transferred from the cultures to the experimental trials using plastic tubes.

Experimental design

The experiment was carried out in a greenhouse during 2012 to evaluate the effectiveness of various BCAs against *F. occidentalis* at canopy and soil level. Cyclamen potted plants (cv. Halios) were used in these experiment. Four potted cyclamen plants with well-developed flowers (pot diameter 20 cm) were put into cages (1m x 1m x 1m). Cages were built with metal layer at the bottom side and the other sides enclosed with mite-proof net, to allow plants illumination and avoid thrips and BCAs escaping. Each plant was infested with about 10 adults and 50 juveniles two weeks prior to the first BCAs application. Plants were placed on greenhouse floor and maintained regularly watered and fertilized during experiment. Climatic conditions in the greenhouse were kept at 18 ± 8°C and 63 % ± 15% R.H.

The experiment was performed applying a factorial design where canopy application of BCAs and soil application of BCAs constituted the two experimental factors. BCAs were introduced on the canopy or the soil following the guidelines provided by producers and

referring to high infestation levels. The factor "Canopy" had four levels: 1) release of *Orius laevigatus* (Thripor-L; Koppert; release rate: 10 individuals/m^2); 2) release of *Neoseiulus cucumeris* (Thripex-V®; Koppert; release rate: 100 individuals/m^2); 3) release of *Amblyseius swirskii* (Swirski-Mite®; Koppert; release rate: 100 individuals/m^2); 4) Control, with no BCAs released on the canopy. The factor "Soil" had three levels: 1) release of *Steinernema feltiae* (Nemasys®; Becker Underwood; release rate: 250,000 individuals/m^2); 2) release of *Macrocheles robustulus* Berlese (Macro-Mite®; Koppert; release rate: 250 individuals/m^2) 4) Control with no BCAs released on soil. A total of 12 treatments each with 4 replicates were compared (Table 1). All BCAs were released within 24 h of their arrival in the laboratory. Predators were released by dispersing the material on the plant canopy or the soil. Nematode release was performed by a drench application of 2 litre/m^2 of nematode suspension.

Prior to BCAs release the population of *F. occidentalis* was estimated by shacking plants canopy onto a white sheet of paper and counting fallen individuals. After BCAs release, the abundance of *F. occidentalis* population and predatory mites was assessed by weekly samples of eight leaves and four flowers per plant. Additionally, visual inspection of plants was used to evaluate the abundance of predatory bugs. Samples were analysed under a dissecting microscope for thrips counting and life stages identification. In order to determine the presence and the persistence of *S. feltiae* and *M. robustulus* about 15 ml of soil were collected from each pot every week and placed inside two 50 ml sterilized vials for a total of 30 ml of soil. One sample from each replicate was used to evaluate the presence of entomoparasitic nematodes using the "*Galleria* bait method" (Zimmerman, 1986), i.e. 3-4 *Galleria mellonella* larvae per soil sample. To evaluate the persistence of *S. feltiae* in the soil we evaluated the infection rate, as the number of *G. mellonella* larvae showing symptoms of *S. feltiae* infection on the total number of larvae introduced in soil samples. The other samples were analysed under dissecting microscope to evaluate the presence of *M. robustulus*. The samples were performed weekly until 35 days from BCAs release**.**

Table 1 - Experimental design with treatments identified by combinations of experimental factors.

Treatment	soil application	canopy application
1	Control	*A. swirskii*
2	Control	*N. cucumeris*
3	Control	*O. laevigatus*
4	Control	Control
5	*S. feltiae*	*A. swirskii*
6	*S. feltiae*	*N. cucumeris*
7	*S. feltiae*	*O. laevigatus*
8	*S. feltiae*	Control
9	*M. robustulus*	*A. swirskii*
10	*M. robustulus*	*N. cucumeris*
11	*M. robustulus*	*O. laevigatus*
12	*M. robustulus*	Control

Statistical analysis

Data on *F. occidentalis* population observed on plants prior to BCAs release were analysed with a a Restricted Maximum Likelihood (REML) ANOVA model with the MIXED procedure of SAS (SAS Institute, 1999) and differences among treatments were evaluated with an F test ($\alpha = 0.05$). Data on *F. occidentalis* population and predators observed on flowers and leaves after BCAs release were analysed with a Restricted Maximum Likelihood (REML) repeated measures ANOVA model with the MIXED procedure of SAS (SAS Institute, 1999). Densities of *F. occidentalis* and predators observed on flowers and leaves were analysed separately and considered as response variables with repeated measures made at different times, i.e. sampling dates. Using a F test ($\alpha = 0.05$) we evaluated the effect of experimental factors, time and their interactions. Differences among treatments were evaluated using a t-test to the least-square means ($\alpha = 0.05$). Slice option was used to partition F test of significant interactions between experimental factors. The Kenward-Roger method was used for degrees of freedom estimation. According to Aikaike's Information Criterion, first-order autoregressive proved to be the best fitting covariance structure for correlating different sampling dates. Data were checked for analysis assumptions and data recorded on

flowers were used as untransformed, while data from leaves were square root transformed.

Results

Phytophagous thrips

Prior to BCAs releases no differences in terms of *F. occidentalis* densities were found among treatments (Table 2; Figure 1). On flowers the number of thrips peaked in the control 15 days from the beginning of the experiment, and then declined (Figure 2). After BCAs release, *F. occidentalis* population were influenced by BCA applications on canopy and soil and by time (Table 3). Considering treatments applied at the canopy level, *F. occidentalis* infestation level was higher in the control compared to BCAs release treatments (vs. *N. cucumeri*s: $t_{59.5} = 5.69$; $P < 0.001$; vs. *O. laevigatus*: $t_{59.5} = 3.11$; $P = 0.01$; vs. *A. swirskii*: $t_{59.5} = 6.57$; $P < 0.001$; Figure 2). Lower thrips populations were found in *A. swirskii* compared to *O. laevigatus* release ($t_{59.5} = 3.11$; $P = 0.02$; Figure 2) and on *N. cucumeris* compared to *O. laevigatus* release ($t_{59.5} = 2.58$; $P = 0.01$; Figure 2). No differences emerged between *A. swirskii* and *N. cucumeris* releases ($t_{59.5} = 0.88$; $P = 0.38$; Figure 2). Among the treatments applied at soil level, *F. occidentalis* population was reduced by both treatments (Table 3; Figure 3) compared to the control (vs. *M. robustulus* $t_{59.5} = 3.77$; $P < 0.001$; vs. *S. feltiae*: $t_{59.5} = 2.31$; $P = 0.024$; Figure 3). No differences emerged between the two BCAs released on soil ($t_{59.5} = 1.47$; $P = 0.148$; Figure 3). A significant interaction “soil * time” was observed (Table 2). The effect of time was significant in *S. feltiae* treatment ($F_{3, 59.5} = 4.26$; $P = 0.001$) where a dramatic decrease was observed from 21 days after release onwards (Figure 3). No effect of time was observed in the other two soil treatments (Control: $F_{2, 59.5} = 1.71$; $P = 0.153$; *M. robustulus*: $F_{2, 59.5} = 1.16$; $P = 0.331$; Figure 3).

F. occidentalis populations occurred at lower levels on leaves than on flowers (Figure 4). A significant effect of BCAs released on canopy and soil were observed on *F. occidentalis* on leaves (Table 3; Figure 4) but a significant interaction between the two experimental factors was observed (Table 4). This effect was also affected by time (Table 3; Figure 4). The effect of BCAs release on soil was significant only where no BCAs were

applied to the canopy (Control: $F_{2, 74.3} = 16.09$; $P < 0.001$; *N. cucumeris* $F_{2, 74.3} = 1.39$; $P = 0.256$; *O. laevigatus*: $F_{2, 74.3} = 0.28$; $P = 0.754$; *A. swirskii*: $F_{2, 74.3} = 0.7$; $P = 0.498$; Figure) and *viceversa* (Control: $F_{2, 74.3} = 13.69$; $P < 0.001$; *S. feltiae* $F_{2, 74.3} = 2.93$; $P = 0.091$; *M. robustulus*: $F_{2, 74.3} = 0.49$; $P = 0.692$; Figure 4). The application of BCAs to canopy determined a reduction of *F. occidentalis* (*N. cucumeris:* $t_{74.3} = 5.03$; $P < 0.001$; *O. laevigatus*: $t_{74.3} = 5.29$; $P < 0.001$; *A. swirskii*: $t_{74.3} = 5.35$; $P < 0.001$; Figure 4) and no differences were observed among these treatments (*N. cucumeris* vs. *O. laevigatus*: $t_{74.3} = 0.27$; $P = 0.791$; *N. cucumeris* vs. *A. swirskii*: $t_{74.3} = 0.33$; $P = 0.743$; *O. laevigatus* vs. *A. swirskii*: $t_{74.3} = 0.06$; $P = 0.955$; Figure 4). A reduction in *F. occidentalis* population was also induced by the application of BCAs on the soil (*S. feltiae* $t_{74.3} = 4.42$; $P = 0.002$; *M. robustulus*: $t_{74.3} = 5.29$; $P < 0.001$; Figure 4). No differences emerged between the two BCAs applied on the soil ($t_{74.3} = 0.88$; $P = 0.3834$; Figure 4).

Table 2 - Results of ANOVA performed on *F. occidentalis* abundance observed on plants prior to BCAs release.

Effect	Num DF	Den DF	F value	Pr>F
CANOPY	3	36	0.41	0.7437
SOIL	2	36	0.26	0.7639
CANOPY*SOIL	6	36	0.3	0.9329

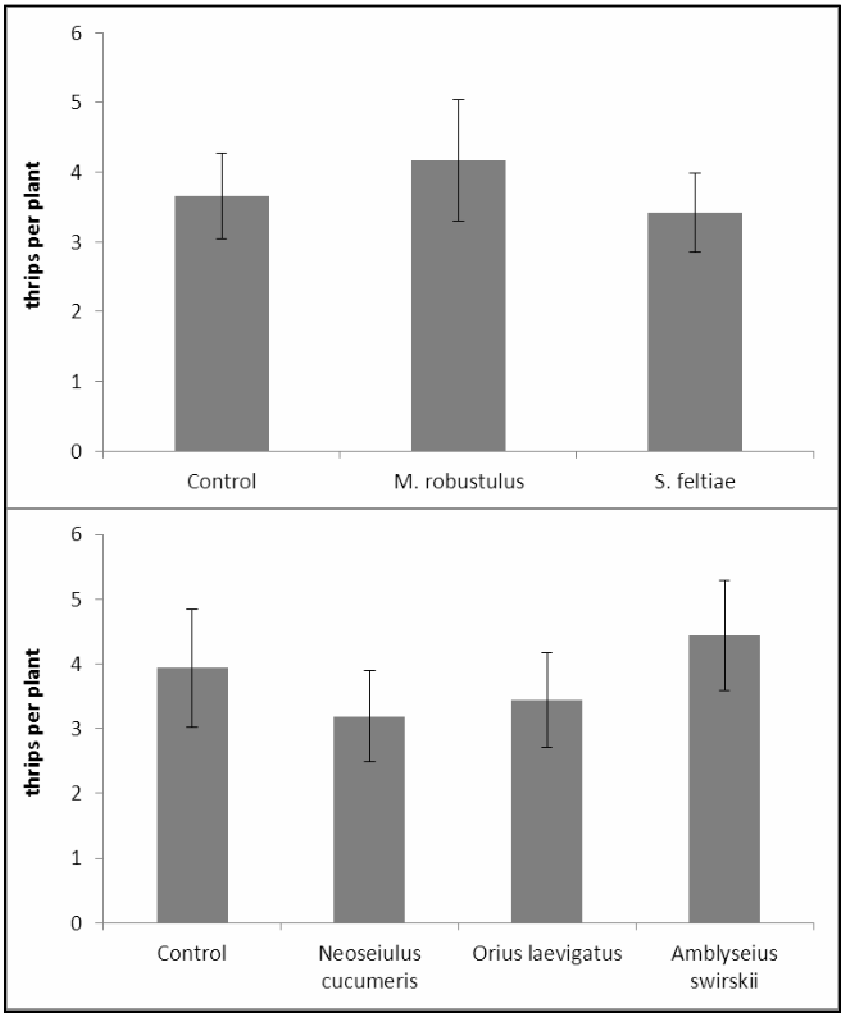

Figure 1 - *F. occidentalis* population abundance observed on plants prior to BCAs release.

Table 3 - Results of factorial repeated measures ANOVA performed on *F. occidentalis* abundance observed on flowers and leaves after BCAs release.

Effects	F	d.f.	P
Frankliniella occidentalis on flowers			
Canopy	17.45	3 ; 59.5	< 0.001
Soil	7.24	2 ; 59.5	0.002
Canopy * Soil	1.56	6 ; 59.5	0.174
Time	6.11	4 ; 139.0	< 0.001
Canopy * Time	0.64	12 ; 148.0	0.802
Soil * Time	4.71	8 ; 146.0	< 0.001
Soil * Canopy * Time	1.11	24 ; 147.0	0.342
Frankliniella occidentalis on leaves			
Canopy	9.15	3 ; 74.3	< 0.001
Soil	7.58	2 ; 74.3	0.001
Canopy * Soil	3.63	6 ; 74.3	0.003
Time	0.68	4 ; 133.0	0.609
Canopy * Time	1.28	12 ; 145.0	0.234
Soil * Time	0.82	8 ; 142.0	0.589
Soil * Canopy * Time	1.68	24 ; 145.0	0.034

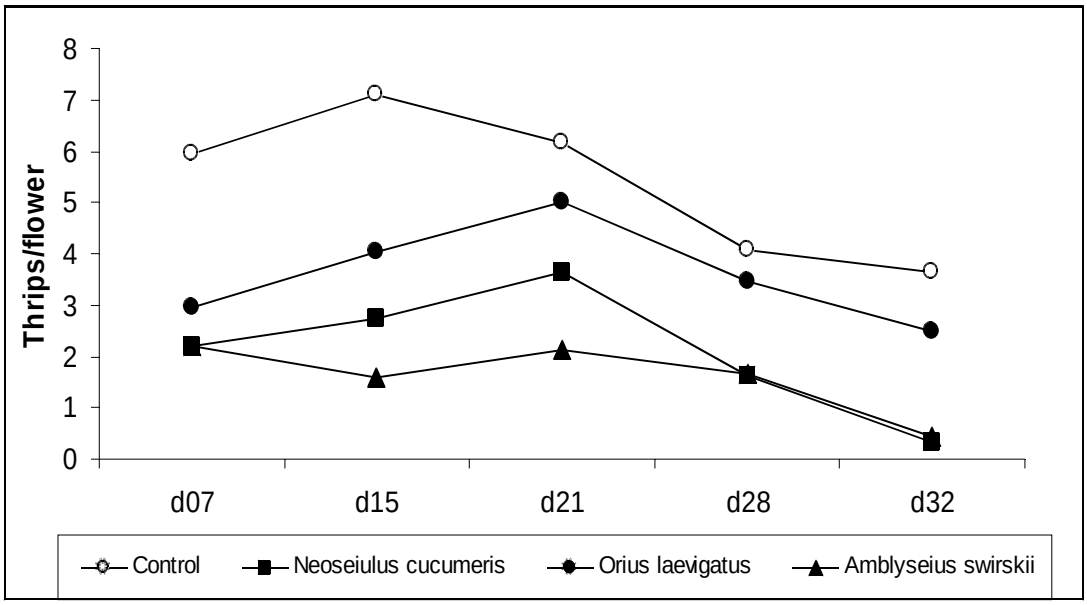

Figure 2 - *F. occidentalis* population abundance observed on cyclamen flowers in treatments characterized by different treatments on the canopy and after BCAs release.

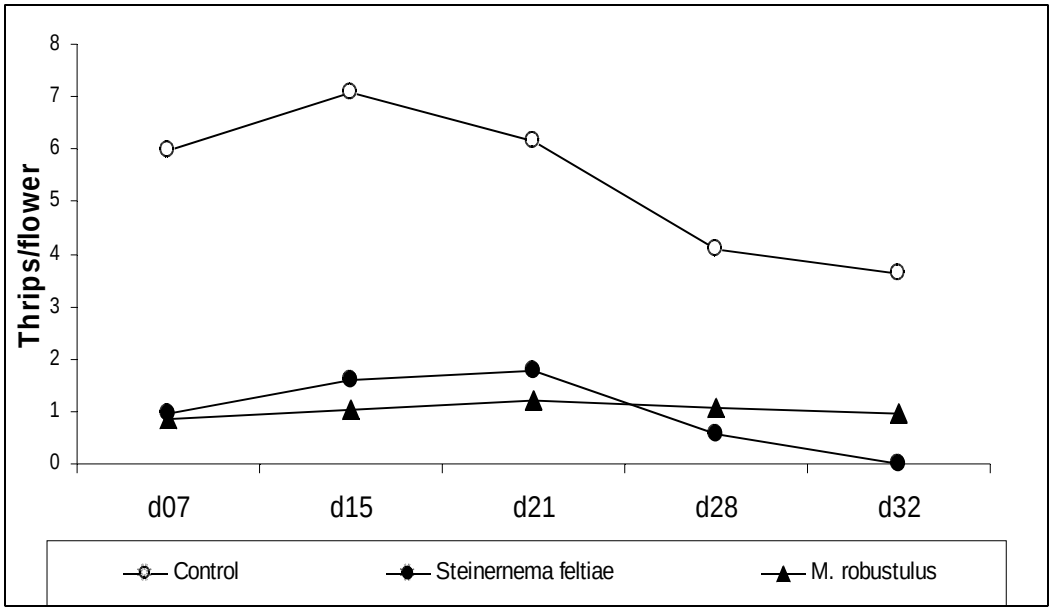

Figure 3 – *F. occidentalis* population abundance observed on cyclamen flowers in treatments characterized by different treatments on the soil, and after BCAs release.

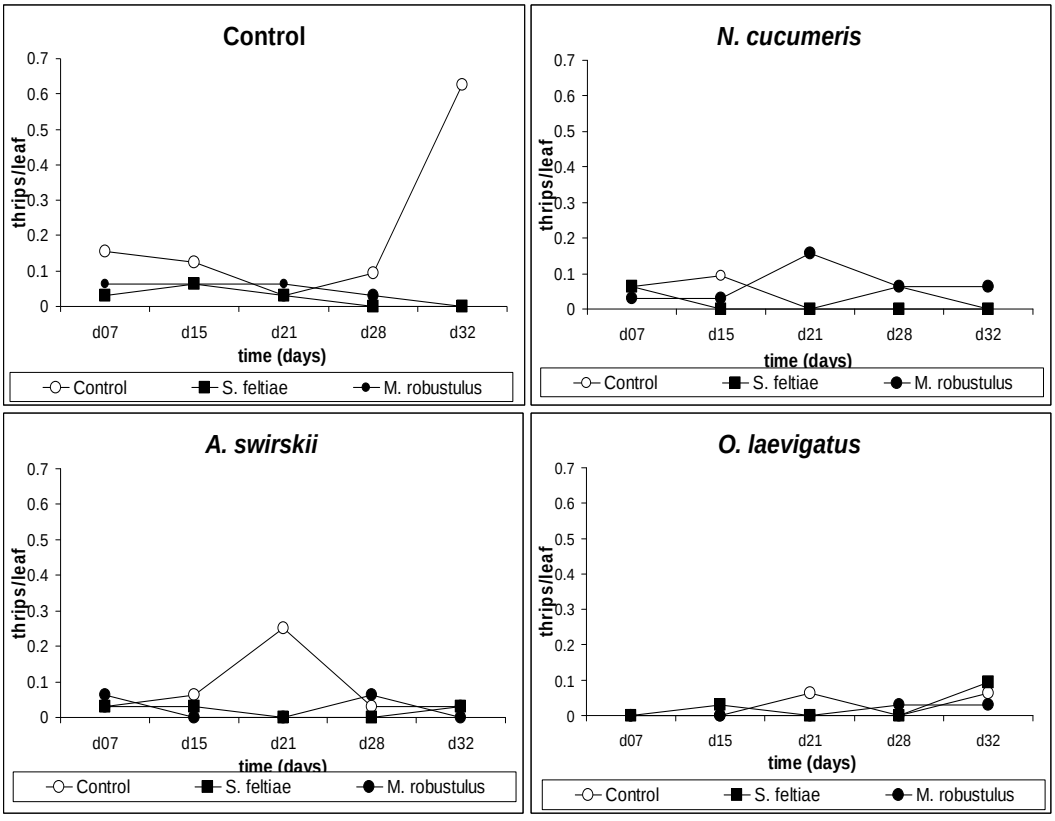

Figure 4 - *F. occidentalis* population abundance observed on cyclamen leaves in treatments characterized by different treatments on the canopy and the soil, and after BCAs release.

Table 4 - Results of factorial repeated measures ANOVA performed on predatory mites abundance observed on flowers and leaves after BCAs release.

Effects	F	d.f.	P
Predatory mites on flowers			
Canopy	42.14	3 ; 61.7	< 0.001
Soil	0.98	2 ; 61.7	0.381
Canopy * Soil	1.38	6 ; 61.7	0.238
Time	0.89	4 ; 133.0	0.471
Canopy * Time	1.14	12 ; 144.0	0.330
Soil * Time	1.05	8 ; 141.0	0.404
Soil * Canopy * Time	0.83	24 ; 144.0	0.693
Predatory mites eggs on flower			
Canopy	2.02	3 ; 63.6	0.120
Soil	0.25	2 ; 63.6	0.778
Canopy * Soil	0.25	6 ; 63.6	0.957
Time	0.87	4 ; 130.0	0.485
Canopy * Time	1.36	12 ; 142.0	0.192
Soil * Time	0.87	8 ; 139.0	0.540
Soil * Canopy * Time	0.87	24 ; 143.0	0.646
Predatory mites on leaves			
Canopy	6.31	3 ; 64.4	0.001
Soil	2.43	2 ; 64.4	0.096
Canopy * Soil	1.17	6 ; 64.4	0.334
Time	1.22	4 ; 140.0	0.304
Canopy * Time	0.72	12 ; 149.0	0.730
Soil * Time	1.20	8 ; 147.0	0.303
Soil * Canopy * Time	1.43	24 ; 148.0	0.104

Biological control agents

The presence of *N. cucumeris* and *A. swirskii* was observed on flowers and leaves (Figure 5), whereas the occurrence of *O. laevigatus* was never observed. A single *O. laevigatus* nymph was found in a replication of release treatments 7 days from the beginning of experiment. The presence of predatory mites on flowers was higher on the respective release treatments compared to other treatments (Table 4; *N. cucumeris* vs. Control: $t_{61.7} = 2.57$; $P = 0.007$; *N. cucumeris* vs. *O. laevigatus*: $t_{61.7} = 2.42$; $P = 0.001$; *A. swirskii* vs. Control: $t_{61.7} = 9.87$; $P < 0.001$; *A. swirskii* vs. *O. laevigatus*: $t_{61.7} = 9.54$; $P < 0.001$). *A. swirskii* reached higher population levels compared to *N. cucumeris* ($t_{61.7} = 7.13$;

P < 0.001). No predatory mites were observed in the control and *O. laevigatus* treatment ($t_{61.7} = 0.00$; P = 1.000). The presence of predatory mite eggs was found on flowers in their release treatments but at a very low levels and without differences (Table 4; data not reported).

On leaves only *N. cucumeris* and *A. swirskii* were observed among predators, but at lower level compare to flowers (Figure 6). Their presence was higher on their release treatments compared to other treatments (Table 3; *N. cucumeris* vs. Control: $t_{64.4} = 3.02$; P = 0.021; *N. cucumeris* vs. *O. laevigatus*: $t_{64.4} = 3.02$; P = 0.021; *A. swirskii* vs. Control: $t_{64.4} = 3.13$; P = 0.015; *A. swirskii* vs. *O. laevigatus*: $t_{64.4} = 3.13$; P = 0.015; Figure 6). No differences were observed between the density of the two predatory mites ($t_{64.4} = 0.11$; P = 0.914; Figure 6). No predators were observed in the control and *O. laevigatus* treatments ($t_{64.4} = 0.00$; P = 1.000 ; Figure 6).

In soil samples the presence of *M. robustulus* was observed until the end of the experiment in the respective release treatment at an average density of 3 mites per 15 ml of soil. Regarding *S. feltiae*, its presence was detected in soil using the "*Galleria* bait method" for the entire experiment (data not reported) with an average infection rate of 85 – 100% in *G. mellonella* larvae.

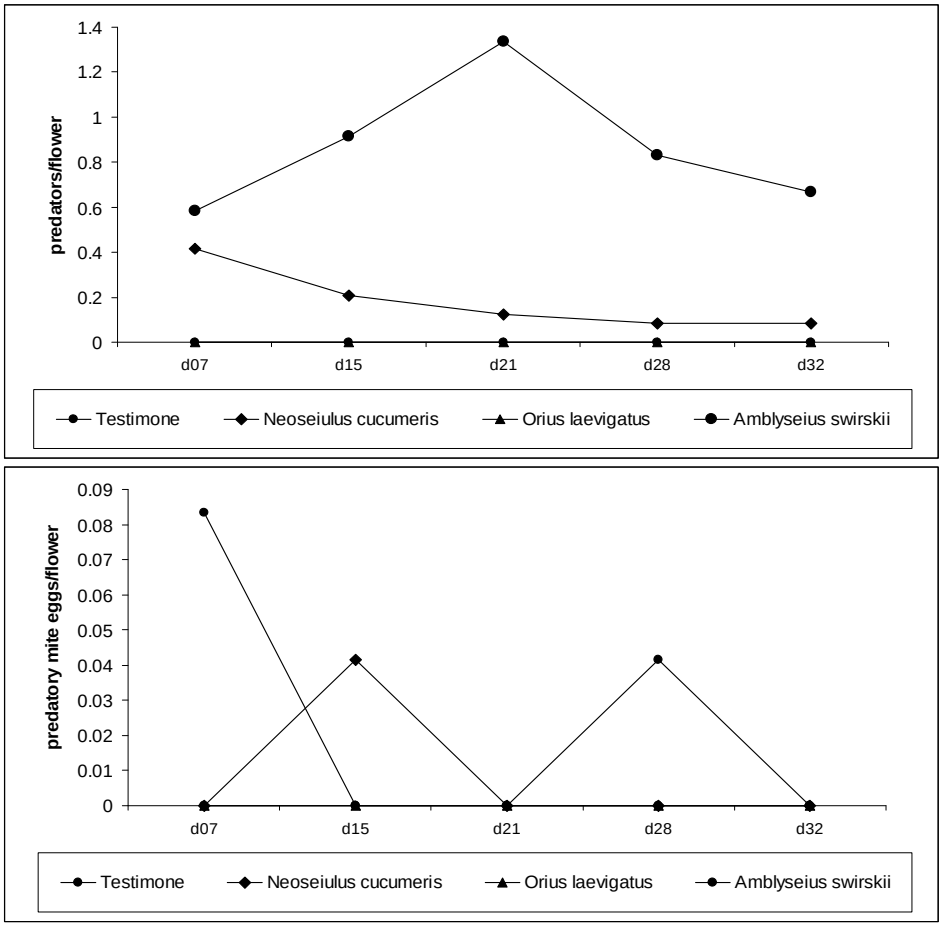

Figure 5 - Abundance of predatory mites observed on cyclamen flowers in treatments characterized by different treatments on canopy and after BCAs release.

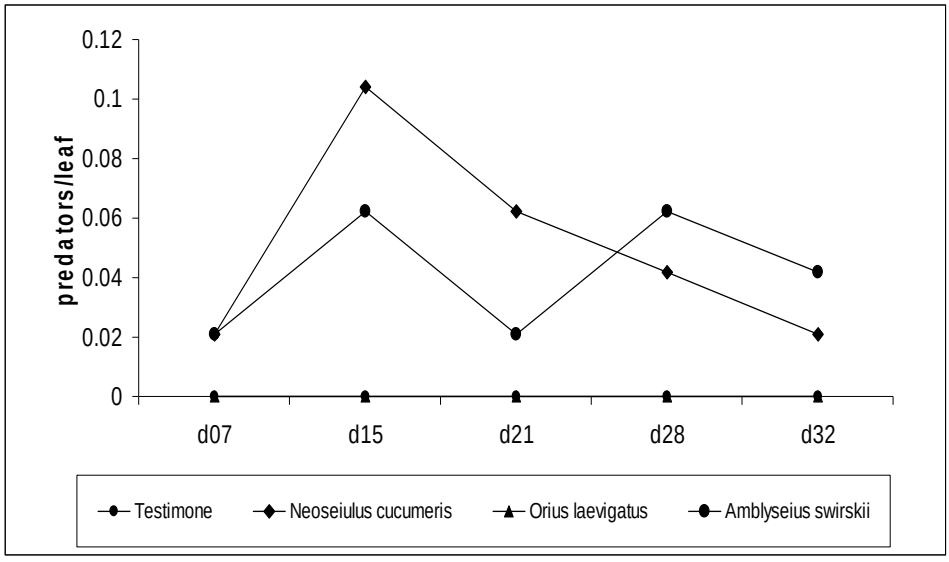

Figure 6 - Abundance of predatory mites observed on cyclamen leaves in treatments characterized by different treatments on canopy and after BCAs release.

Discussion

The presence of *F. occidentalis* was higher on flowers than on leaves probably because thrips found food resources (i.e., pollen) and oviposition sites in the former (de Jager et *al.*, 1993; Gerin et *al*., 1999, Chau et *al*., 2005; Cloyd, 2009). It should be stressed that flowers are of primary importance for cyclamen commercialization. Feeding activity *F. occidentalis* on flowers can determine discoloration and deformation with a great reduction in commercial value of this crop. The use of BCAs reduced *F. occidentalis* populations on flowers and predatory mite released on the canopy performed better. BCAs released on the canopy reduced thrips abundance on leaves at similar levels among predators. Both phytoseiids were found inside flowers, but *A. swirskii* was more abundant than *N. cucumeris*. However, no differences were reported between the overall control level obtained by the two predatory mites.

The two predatory mites can feed on the same thrips stages (Bakker and Sabelis, 1989; Wimmer et *al*. 2008; Arthurs et al., 2009; Cuthbertson et *al*., 2012); our results contrast with a previous comparative study performed on cucumber where *A. swirskii* showed higher performance compared to *N. cucumeris* (Messelink et *al*., 2006). In this paper the number of *A. swirskii* found at the end of experiment were about 9-fold higher than *N. cucumeris,* and the infestation level found after *A. swirskii* release was about 5-fold lower

than that found after *N. cucumeris* release. On the other hand, Buitenhuis et *al.* (2010) found that predation rate and oviposition rate of *N. cucumeris* feeding on *F. occidentalis* first instars were higher than those exhibited by *A. swirskii* feeding on the same prey. No differences were observed between the predation rate of the two predatory mites on *Thrips palmi* Karny and *Thrips nigropilosus* Uzel on cucumber leaf discs (Cuthbertson et *al*., 2012). Equal performance in laboratory and better performance of *A. swirskii*, at plant level, were found by Arthurs et al. (2009) comparing the effect of *N. cucumeris* and *A. swirskii* in the control of chilli thrips *Scirtothrips dorsalis* Hood on pepper. They found no differences in consumption rate and fecundity of the two predators feeding thrips in laboratory, but on plants in greenhouse and landscape conditions *A. swirskii* performed better.

It should be noted that in studies performed at plant level, the effect of predators was assessed on *F. occidentalis* infestation on leaves. In another study differences in *F. occidentalis* control by the two predators were lower on leaves than on flowers (van Houten et *al*., 2005). In a previous study, *F. occidentalis* was categorized as suboptimal (e.g., compared to pollen and whiteflies) food source for *A. swirskii* (Wimmer *et al*., 2008). In the same study, authors suggest that the population growth capacity of *A. swirskii* feeding on *F. occidentalis* is not higher than that of *N. cucumeris* on the same prey (by a comparison with data reported by Castagnoli and Simoni, 1990). Possible explanations of differences observed between the two predatory mites may be related to alternative food availability. These predatory mites are classified as type-III generalist predators (McMurtry and Croft, 1997; McMurtry et *al.*, 2013), thus they can feed on various food sources included pollen that is an abundant alternative food in flowers. At our knowledge no direct comparisons on the effect of cyclamen pollen (and other pollen taxa) on the life history parameters of the two predators have been published. Recently two papers have been published by the same laboratory on the effect of various pollen taxa on the life history parameters of the two phytoseiids (Goleva and Zebitz 2013; Ranabhat et *al*., 2013). In these papers *N. cucumeris* and *A. swirskii* were reared with different kinds of pollen under the same conditions. *A. swirskii* showed a higher performance than *N. cucumeris* (in term of mortality and demographic parameters) by feeding on pollen. Results suggest that pollen is a more suitable food source for *A. swirskii* than for *N. cucumeris*. Among generalist phytoseiids it has been observed that predation can be reduced in presence of alternative food sources

(Wei and Walde, 1997; Zemek, 2005). A predator should prefer to exploit a more profitable food and switch to a less profitable when the former is scarce (Murdoch 1969; van Baalen et *al*., 2001).

Hence the outcome of biological control can be influenced by the relative quality and quantity of different food sources (Srinivasu et *al*., 2007). We have no data on the preference of the two predatory mites for thrips or pollen, but life history parameters can provide an estimation of the relative quality/suitability of different food sources for predatory mites (Sabelis, 1985; Dicke et *al*., 1990). According to laboratory data *F. occidentalis* should be equally suitable for the two predators whereas pollen is a more suitable food source for *A. swirskii*. At higher pollen availability, this predator should prefer to feed in this food source resulting distract from predation. On leaves, with lower pollen availability, a higher *A. swirskii* performance in preying *F. occidentalis* is expected. The higher performances in *F. occidentalis* control exhibited by *A. swirskii* compared to *N. cucumeris* seems not related to differences in population growth capacity observed between the two predators, but probably to differences in their behavioral and physiological traits (e.g., Wimmer et *al*., 2008; Zilahi-Balogh et *al*., 2007; Arthurs et al., 2009).

We observed a relatively low performance of *O. laevigatus* when compared with predatory mites. However we were not able to detect predatory bugs after the first week post-release. By looking at the dynamics of *F. occidentalis* on flowers, the reduction of thrips population compared to the control seems to be related to the first week of predatory bug activity; in fact, no further reduction emerged after. This may suggest that *O. laevigatus* was not active for the entire experiment. *F. occidentalis* infestation on leaves was reduced at the same level of predatory mites. On the other hand, *O. laevigatus* controls better than *A. swirskii* thrips infestation on sweet pepper flowers (Weitraub, 2011). Differences in these results could be determined by the architecture of cyclamen flowers that provided a refuge for *F. occidentalis* from *O. laevigatus*. Indeed, host plant features are known to influence predation by anthocorids (e.g., Coll and Ridgway, 1995, Coll et *al*., 1997; Coll and Izraylevich, 1997). The predatory bug was able to feed on thrips outside flowers maybe on those found in senescent flowers, but was unable to reach thrips protected inside fresh flowers during the experiment. No previous data are available on the use of this species in augmentative strategies against *F. occidentalis* on cyclamens.

Limitation in predation of *F. occidentalis* within flowers has been reported for *Orius majusculus* Wolff on chrysanthemum (Brødsgaard and Enkegaard, 2005). The combined release of *Orius insidiosus* Say and *A. swirskii* did not provide additional control of *F. occidentalis* on flowers compared to *A. swirskii* alone (Chow et *al*., 2010). In other studies carried out on the same crop, anthocorids attained a better control of *F. occidentalis* within flowers, but these results are not comparable because of the use of different cultivars and predatory bug species (e.g., Chow et *al*., 2008; Madadi, 2009; Manners, 2013).

BCAs released on the soil provided satisfactory control of *F. occidentalis*. The entomoparasitic nematode in particular determined the extinction of *F. occidentalis* at the end of experiments. These results confirm previous findings using *M. robustulus* (Messelink and van Holsten-Saj, 2008) and *S. feltiae* (Ebbsa et al., 2001; Premachandra et *al*., 2003; Buitenhuis and Shipp, 2005). The effect observed here was determined by a significant pupation of *F. occidentalis* in the soil that exposed thrips to soil-dwelling antagonists.

Using a factorial experiment we were able to detect additive effect of soil and canopy applications. The lack of significant interaction on *F. occidentalis* population density on flowers indicates that release of BCAs on soil and on canopy act independently (Sih et al. 1998). Therefore the addition of the two release strategies will improve the control level of *F. occidentalis*. This is not obvious since in previous results the combined use of predatory mites on canopy and soil did not improve the control of *F. occidentalis* (Wiethoff, 2004). *F. occidentalis* is considered a pest difficult to manage with chemical and biological control measures on ornamental crops. Our findings show that the combined use of BCAs at canopy and soil level against *F. occidentalis* on cyclamens can be a useful strategy for the improvement on biological control.

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Chapter V

Effects of *Beauveria bassiana* on *Frankliniella occidentalis* (Thysanoptera: Thripidae) trough different routes of exposure

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In this work, I collected most of the data, contributed to the statistical analysis and drafted the manuscript.

Abstract

The potential of *Beauveria bassiana* has been tested on several agricultural pest species, included the Western Flower Thrips *Frankliniella occidentalis* Pergande. However, knowledge on *B. bassiana*-thrips interactions is limited. In laboratory bioassays, different developmental stages of *F. occidentalis* (first and second instars, adults) were exposed to residual or topical applications of a *B. bassiana* commercial strain (JW-1, ATCC 74040). Mortality varied according to life stage and type of exposure, reaching maximum levels when the two routes of exposure were combined. By one hand, topical exposure induced the highest mortality of first instars. On the other hand, residual exposure showed a higher impact on second instars and adults. Combined exposures determined the highest mortality rates. Results stress on the importance to favour the contact of thrips with *B. bassiana* conidia to obtain a satisfactory control. In addition, exposure to *B. bassiana* determined some effects on thrips development from immature stages to prepupae. Treated first and second instars showed a reduced development rate when exposed to *B. bassiana* residues; whereas topical exposure did not cause any effect on development. The significant reduction in thrips survival after *B. bassiana* applications suggests that entomopathogenic fungi can be considered an alternative to synthetic pesticides. Implications for Integrated Pest Management (IPM) are discussed.

Introduction

The Western Flower Thrips *Frankliniella occidentalis* Pergande (Thysanoptera: Thripidae) is a major pest of ornamentals and vegetables, in particular in protected systems, over the world. It can damage flowers, fruits, leaves and shoots by feeding and egg-laying; moreover, it can transmit tospoviruses (e.g., TSWV and INSV), causing serious crop losses (Arzone *et al.*, 1989; Pappu et *al.*, 2009). Growers usually apply various control measures against this pest based mainly on synthetic insecticides. However, *F. occidentalis* has developed strains resistant to various pesticides and thus chemical control proved to be ineffective in various regions (Immaraju et al., 1992; Jensen, 2000; Bielza et *al.*, 2007; Bielza, 2008). Increasing costs for thrips control and toxicological problems promoted the search for measures alternative to pesticides.

The potential of various predators, parasites (e.g. nematodes), parasitoids and pathogens has been matter of study and some effective biocontrol agents have been identified (Shipp et *al*., 2003, Loomans and van Lenteren, 1995; Sabelis and van Rijn, 1997; Butt and Brownbridge, 1997). For instance, *Beauveria bassiana* (Balsamo) Vuillemin (Hyphomycetes: Moniliaceae) is a well-known pathogen of various insect and mite pests (Rehner, 2005; Inglis et *al*., 2001).

Some laboratory studies have demonstrated the susceptibility of juvenile stages, as well as adults of *F. occidentalis* to *B. bassiana* (Shipp et *al.*, 2003; Abe and Ikegami, 2005; Ugine et *al*., 2005a,b, 2006; Ansari et *al.*, 2008; Gouli et *al.*, 2007; Suhua et *al.*, 2009; Gao et *al.*, 2012). Several environmental factors can influence the effects of *B. bassiana* infection (Doberski, 1981; Inglis et *al*., 1996; Luz and Fargues, 1999; Jacobson et *al.*, 2001; Meyling and Eilenberg, 2007; Mukawa et *al.*, 2011). Pathogenicity is also influenced by developmental thrips stage (Ugine et *al*., 2005a), the sex of adult thrips (Abe and Ikegami, 2005), the host plant (Ugine et *al.*, 2007a) and the level of exposure (Ugine et *al.*, 2005a). Laboratory studies have underlined how different susceptibility to *B. bassiana* can be observed on the same host life stages following different conidia acquisition levels (Fernandez et *al.*, 2001; Behle, 2006; Ugine et al., 2005b). *Beauveria bassiana* formulations can be distributed over the whole canopy or directly into the soil; thrips stages may come into direct or indirect contact with conidia depending on the substrate they colonize (e.g., leaves or soil). They can be involved by primary (topical exposure) and/or secondary (residual exposure) conidia acquisition (Ugine et *al*., 2005a).

The potential susceptibility of different WFT developmental stages to *B. bassiana* infection as a function of different routes of exposure still requires to be investigated as few studies have been conducted on this topic (e.g., Ugine et *al*., 2005a, b). In this work, the susceptibility of different developmental stages of *F. occidentalis* (first and second instars and adults) to increasing levels of exposure to *B. bassiana* was evaluated. Thrips were exposed both to foliar deposits or topical applications of a *B. bassiana* suspension in the laboratory and then confined in holding cells. Moreover, routes of exposure were combined for an overall evaluation. The effects of *B. bassiana* on *F. occidentalis* developmental rate were also studied. Preliminary data have been reported by Boaria et *al*. (2011, 2013).

Materials and methods

Thrips rearing and their selection for experiments

Thrips rearing followed a method described by DeGraff et *al.* (2009) with minor changes (Boaria et al., 2011). They were reared on cucumber fruits, held into rectangular boxes supplied weekly with *Typha latifolia* pollen and replenished by water for assuring optimal humidity conditions. Cucumbers supplied both food source and oviposition sites. Rearing units were kept at room temperature (25±1 °C), 70%±10% relative humidity, 16:8 (L:D). This method allowed to produce a high number of even age thrips to be used for bioassays.

Then, thrips were collected from rearing units using a fine brush and assigned to each treatment according to their developmental stage (first instars, early second instars, late second instars, and adult females). Early from late second instars were discriminated according to the size of the abdomen relative to the head and thorax and the behavioural traits (early second instars fed on leaves whereas late second instars did not feed but moved quickly in the cage in search of suitable sites for pupation).

Bioassay procedure

B. bassiana solution was obtained by a commercial formulation (strain JW-1, ATCC 74040, Naturalis®), where a concentrated fungal conidia solution was mixed with coadjutants. The product contained at least 2.3 x 10^7 conidia/ml and was stored at 4°C. Conidial suspension was prepared mixing 0,15 ml of formulation in 100 ml of sterile deionized water.

The effect of *B. bassiana* was evaluated on first instars, second instars and adult females. The age of individuals was homogenised by collecting the insects from rearing units every 24h. In trials, 2-3 days old French bean leaves were used as a substrate. Bean plants were grown in 15-cm diameter pots under greenhouse conditions at the Department DAFNAE, University of Padua. Before starting with trials, leaves were washed under flushing water and then dipped in 1% NaClO solution for 2 min; then leaves were rinsed under sterilized deionized water. Thrips were confined in holding cells having bean leaves as a substrate following the procedure described by Dennehy et *al.* (1993) for spider mites (Acarina: Tetranychidae) and modified by Duso et *al*. (2008). Four different treatments were

compared according to an increasing level of *B. bassiana* exposure: 1) untreated control; 2) residual exposure (thrips were reared on *B. bassiana* treated leaves); 3) topical exposure (thrips were dipped in a *B. bassiana* solution); 4) residual exposure + topical exposure.

Regarding residual exposure, sterilized bean leaves were dipped in the *B. bassiana* solution for 30 s and left to dry under sterile conditions. Then, leaves were added to the holding cells as substrate. Untreated thrips were taken from rearing boxes using a camel brush and confined into holding cells.

Concerning topical exposure thrips were immersed in the *B. bassiana* solution using the micro-immersion bioassay (Dennehy *et al*. 1993; Castagnoli *et al*. 2005). Thrips were then drawn into small pipette tip, and successively, the *B. bassiana* solution was drawn up, immersing the thrips for 30 s. The thrips were ejected from the pipette, dried on filter paper in sterile conditions, and transferred singly into holding cells using a fine brush. In combined exposure experiments treated thrips were confined into holding cells having *B. bassiana* treated leaves.

Five thrips were introduced into each holding cell. The latter were maintained under controlled climatic conditions (23°C, 90% R.H. and 15:9 L:D). Each treatment comprised ten replicates of five thrips each. Holding cells were daily monitored under a dissecting stereoscope to assess the number of alive and dead individuals, as well as their developmental stage. Escaped or flattened individuals were considered.

Dead individuals were transferred on sterilized moistened filter paper into 5-cm diameter Petri dishes for fungi identification. Petri dishes were sealed with parafilm and incubated in darkness at 25°C and 90% to favour fungal sporulation and identification. Cadavers either without mycosis or characterized by problems in the identification of pathogens even after 10 days from thrips transfer, were put in 8-cm diameter Petri dishes containing PDA solution (39g/l). Conidia need at least 9-18 h for germination, at optimal temperature and relative humidity levels (Luz and Farguez, 1998; Fernandez et *al*., 2001). Death from fungal infection was confirmed by observing characteristic fungal eruption from cadavers and subsequent sporulation (Deseo and Rovesti, 1992). The identity of pathogens was performed at the compound microscope (400x) where conidia characters were analyzed following description reported by Barnett and Hunter (1998).

Statistical analysis

Data on mortality of *F. occidentalis* exposed to *B. bassiana* through different routes of exposure observed after three, six and nine days were analysed using a factorial logistic regression models. Separated analyses were run for each developmental stage. The analyses were performed using the GENMOD procedure of SAS (SAS Institute, 1999). The effect of each experimental factor was evaluated with a Likelihood–ratio G test ($\alpha = 0.05$). Then, the interactions among the different routes of exposure were investigated.

The effect of a single route of exposure when combined with the others performing a Wald χ^2 test within the LSMEAN statement (SAS Institute, 1999) was partitioned. Abbott (1925) mortality was also calculated.

To evaluate the effect of *B. bassiana* through different routes of exposure on the development of surviving *F. occidentalis* juveniles, a factorial ANOVA model using the MIXED procedure of SAS (SAS Institute, 1999) was used. For each development stage considered in this study, the time (days) needed for the development to the following stage (i.e., from first to early second instars, from early second instars to prepupae and from late second instars to prepupae) was considered as dependent variable in this analysis. In this analysis residual and topical exposure were considered as experimental factors and their interaction was also included in the models and their effects evaluated with an F test ($\alpha = 0.05$). To evaluate the differences between treatments a t test ($\alpha = 0.05$) was also applied to the least square means. Data were checked for homogeneity of variance and were log x + 1 transformed.

Results

Experimental procedure

The experimental procedure applied in bioassays showed to be reliable and not very time consuming. Exposure to *B. bassiana* in holding cells was limited to treated leaf surface simulating a realistic environmental scenario. Maximum mortality rates in untreated control were 7.7% for first instars, 3.9% for early second instars, 15% for late second instars and 7.4% in adults. Escaping in the control was insignificant in trials with first instars and late second instars, and 4% for early second instars and adults.

Effects of routes of exposure on thrips mortality

The survival of thrips first instars was reduced by topical exposure to *B. bassiana* three days after the application of the entomopathogenic fungus (Table 1; Figure 1). Six days after *B. bassiana* application, topical and residual exposures caused a significant effect on first instars (Table 1; Figure 1). A significant interaction "topical exposure * residual exposure" and no differences in mortality between single routes of exposure, as well as between single routes of exposure and their combination, were found (Table 1; Figure 1). The effect of topical and residual exposure on first instars was confirmed nine days after the application of *B. bassiana* (Table 1; Figure 1).

A reduction in early second instars survival was due to residual exposure to *B. bassiana* after six and nine days from application; topical exposure was not associated to significant results in terms of survival (Table 1; Figure 2). No significant interaction was found for this thrips stage. *B. bassiana* induced a significant mortality of late second instars in both routes of exposure and this effect was significant three days from application onwards (Table 1; Figure 3). No significant interactions were found (Table 1)

A reduction in survival was also observed for *F. occidentalis* adults exposed to *B. bassiana* through both routes of exposure. This effect was evidenced six days from application and was confirmed later on (Table 1). Significant interactions between residual and topical exposure were observed six and nine days after *B. bassiana* applications: residual exposure determined higher mortality compared to topical exposure and this effect was not different from the combination of topical and residual exposures (Table 1; Figure 4).

Table 1 - Results of factorial logistic regression of mortality observed on *F. occidentalis* exposed to *B. bassiana.*

Time from application	Source of variation	G	P
first instar larvae			
3 days	Topical exposure	10.03	0.0015
	Residual exposure	3.04	0.0813
	Topical exp. * Residual exp.	2.88	0.0895
6 days	Topical exposure	6.59	0.0102
	Residual exposure	5.26	0.0218
	Topical exp. * Residual exp.	5.13	0.0236
9 days	Topical exposure	41.16	< 0.001
	Residual exposure	7.60	0.0058
	Topical exp. * Residual exp.	2.80	0.0940
early second instar larvae			
3 days	Topical exposure	1.28	0.2576
	Residual exposure	3.03	0.0817
	Topical exp. * Residual exp.	2.37	0.1240
6 days	Topical exposure	0.00	0.9752
	Residual exposure	30.38	< 0.001
	Topical exp. * Residual exp.	0.11	0.7434
9 days	Topical exposure	1.17	0.2787
	Residual exposure	31.35	< 0.001
	Topical exp. * Residual exp.	0.93	0.3352
late second instar larvae			
3 days	Topical exposure	5.66	0.0173
	Residual exposure	4.22	0.0400
	Topical exp. * Residual exp.	1.54	0.2153
6 days	Topical exposure	5.72	0.0167
	Residual exposure	10.39	0.0013
	Topical exp. * Residual exp.	2.38	0.1232
9 days	Topical exposure	6.55	0.0105
	Residual exposure	26.45	< 0.001
	Topical exp. * Residual exp.	0.38	0.5371
adults			
3 days	Topical exposure	0.32	0.5725
	Residual exposure	0.32	0.5725
	Topical exp. * Residual exp.	2.66	0.1027
6 days	Topical exposure	9.85	0.0017
	Residual exposure	39.66	< 0.001
	Topical exp. * Residual exp.	10.52	0.0012
9 days	Topical exposure	14.28	0.0002
	Residual exposure	44.09	< 0.001
	Topical exp. * Residual exp.	6.53	0.0106

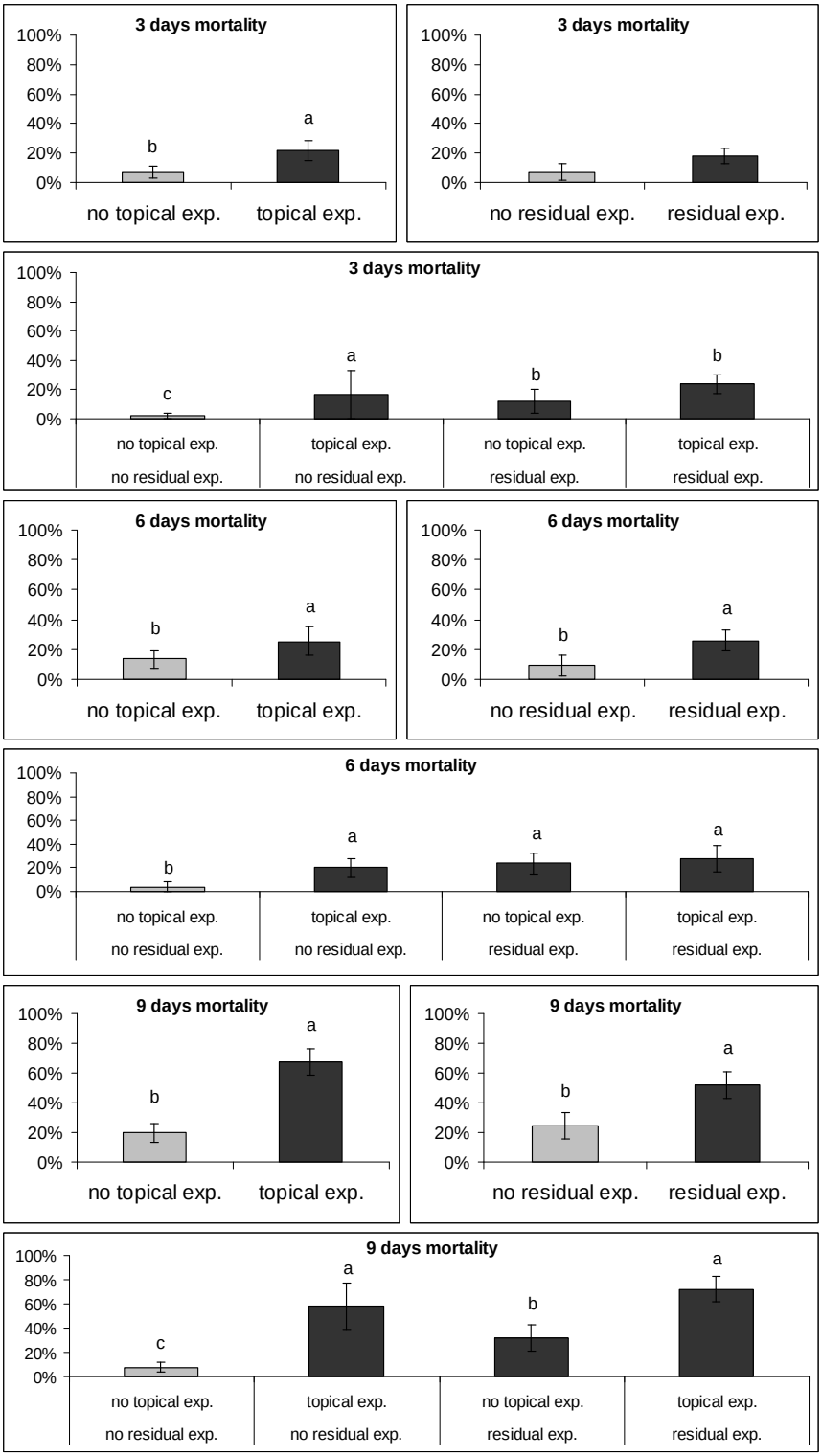

Figure 1 - Mortality of *F. occidentalis* first instars exposed to *B. bassiana* trough different routes of exposure. Different letters indicate significant differences at Wald χ^2 test to the least-square means ($\alpha = 0.05$).

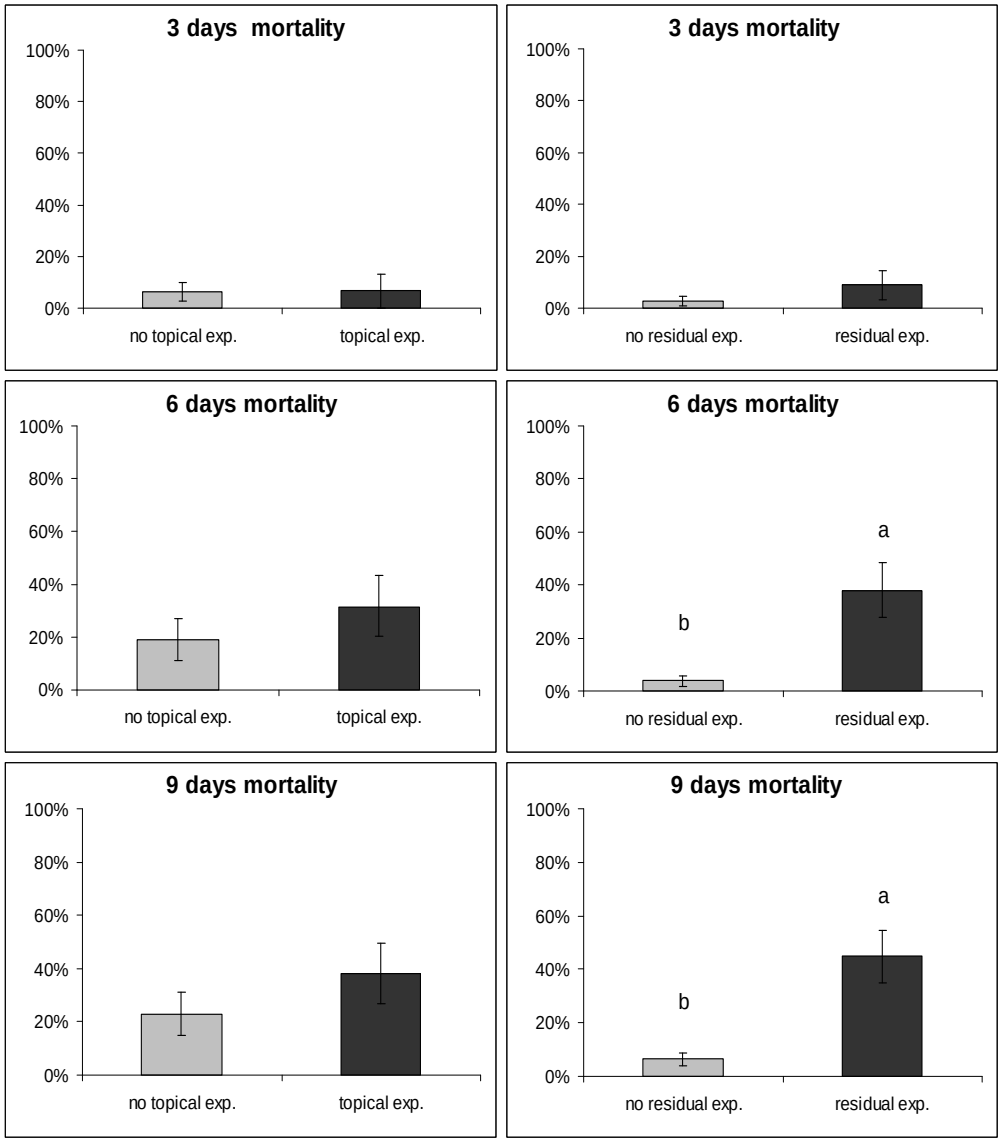

Figure 2 - Mortality of *F. occidentalis* early second instars exposed to *B. bassiana* trough different routes of exposure. Different letters indicate significant differences at Wald χ^2 test to the least-square means ($\alpha = 0.05$).

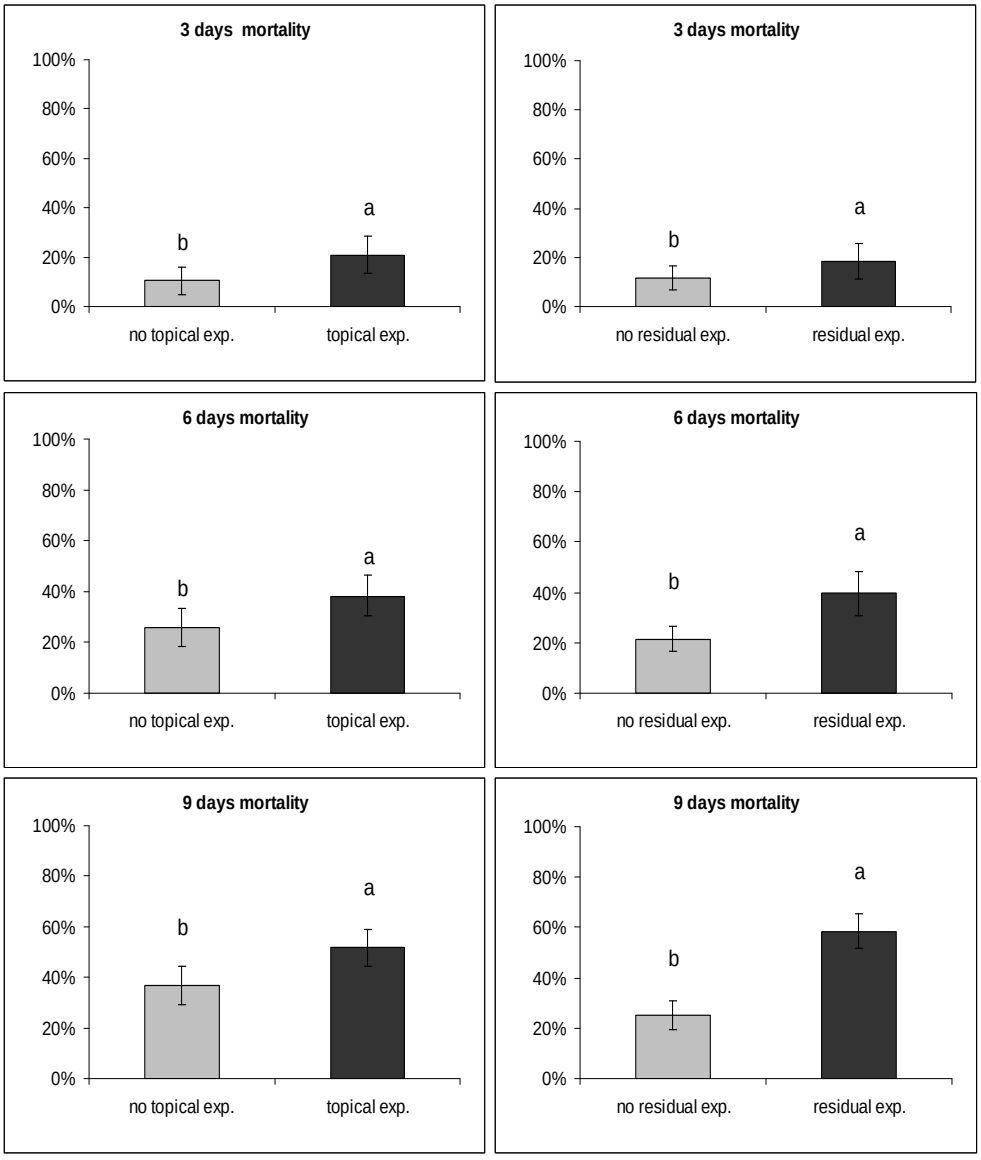

Figure 3 - Mortality of *F. occidentalis* late second instars exposed to *B. bassiana* trough different routes of exposure. Different letters indicate significant differences at Wald χ^2 test to the least-square means ($\alpha = 0.05$).

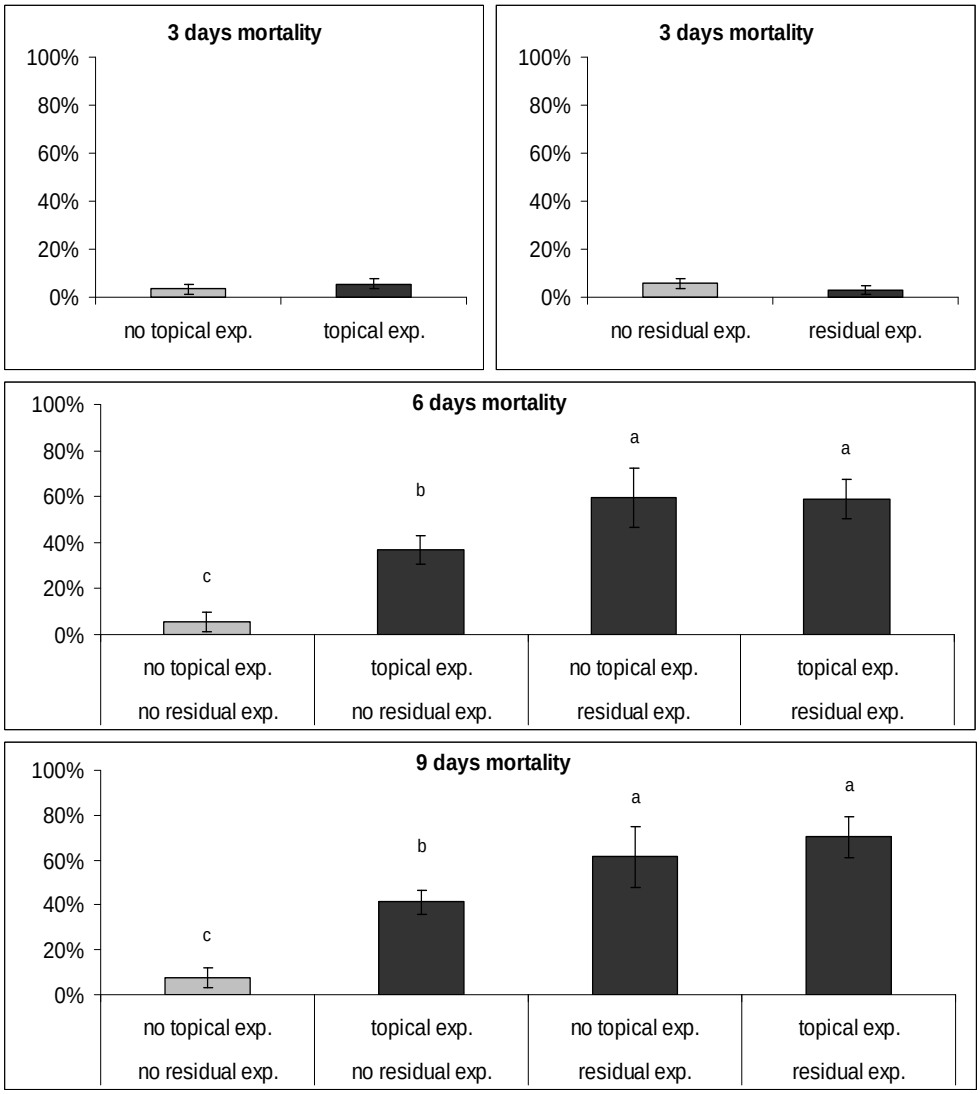

Figure 4 - Mortality of *F. occidentalis* adult females exposed to *B. bassiana* trough different routes of exposure. Different letters indicate significant differences at Wald χ^2 test to the least-square means ($\alpha = 0.05$).

Corrected mortality after exposure to Beauveria bassiana

Results expressed in terms of corrected mortality are summarized in Figure 5. Mortality increased over time regardless of the routes of exposure. First instars were more affected by topical than residual exposure. The combination of exposures produced higher mortality than single treatments. An opposite situation occurred for early second instars where residual exposure displayed a higher mortality than topical exposure. Combined exposures slightly increased mortality. Regarding late second instars, residual exposure induced a

higher mortality than topical exposure and their combination determined additional effects. A similar trend was reported for adults where *B. bassiana* effects reached the highest levels.

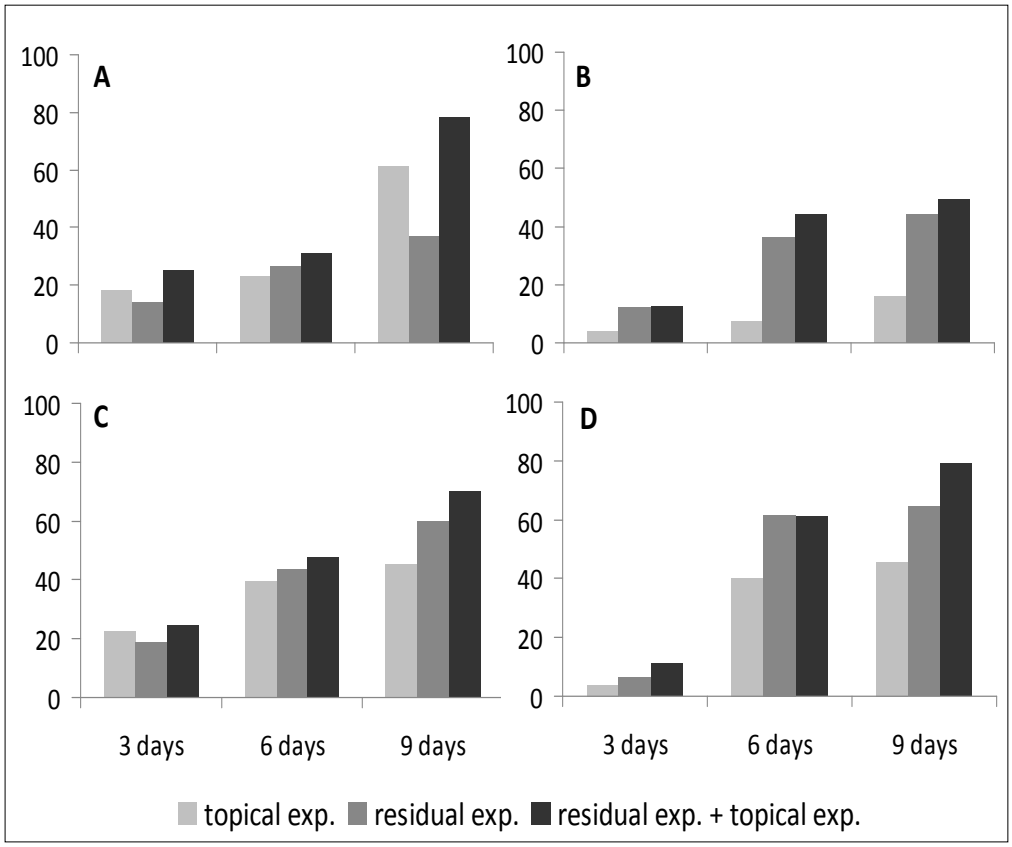

Figure 5 - Corrected mortality (Abbott, 1925) observed on different *F. occidentalis* developmental stages (A: first instars; B: early second instars; C: late second instars; D: adult females) exposed to *Beauveria bassiana.*

Effects of Beauveria bassiana on thrips developmental times

Exposure to *B. bassiana* did not affect developmental times from first to second instar thrips (Table 3; Figure 5). However, residual exposure to *B. bassiana* induced a faster development of early and late second instars into prepupae (Table 3; Figures 6-7). The effect of topical exposure on development of second instars was never significant (Table 3; Figures 6-7).

Table 2 - Effect of *B. bassiana* exposure on developmental times of *F. occidentalis* immatures.

Treated stage	Effect	Num DF	Den DF	F Value	Pr > F
First instars	Residual exposure	1	16.8	0.18	0.68
	Topical exposure	1	22.8	1.32	0.263
	Topical exp. * Residual exp.	1	18.5	0.73	0.404
Early second instars	Residual exposure	1	26	4.89	0.036
	Topical exposure	1	26	3.77	0.063
	Topical exp. * Residual exp.	1	26	0.38	0.545
Late second instars	Residual exposure	1	14.4	6.01	0.028
	Topical exposure	1	16.5	0.07	0.793
	Topical exp. * Residual exp.	1	14.5	2.45	0.139

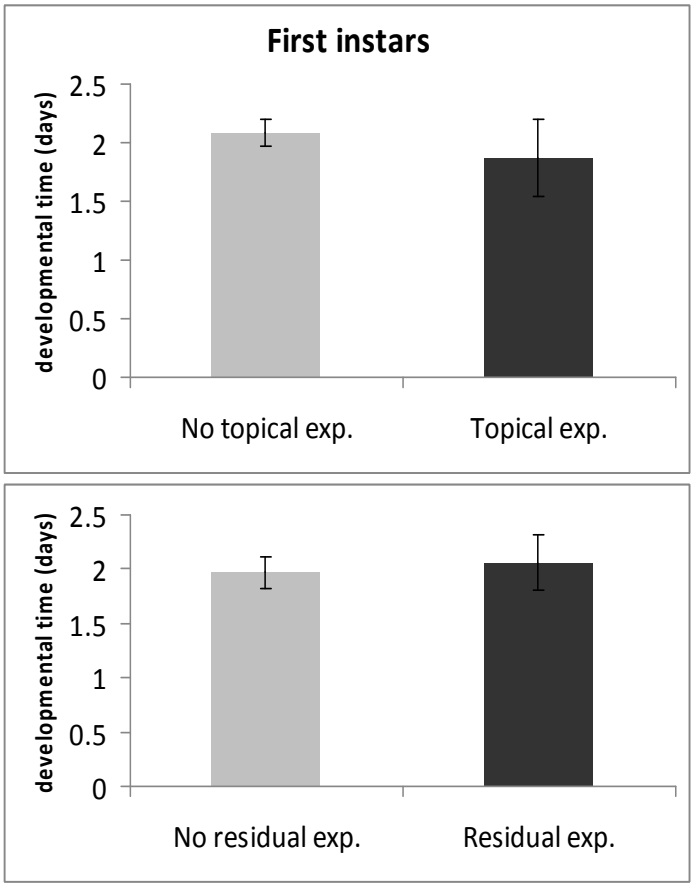

Figure 6 - Developmental times of *F. occidentalis* first instars to early second instars. Different letters indicate significant differences at t test to the least square means ($\alpha = 0.05$).

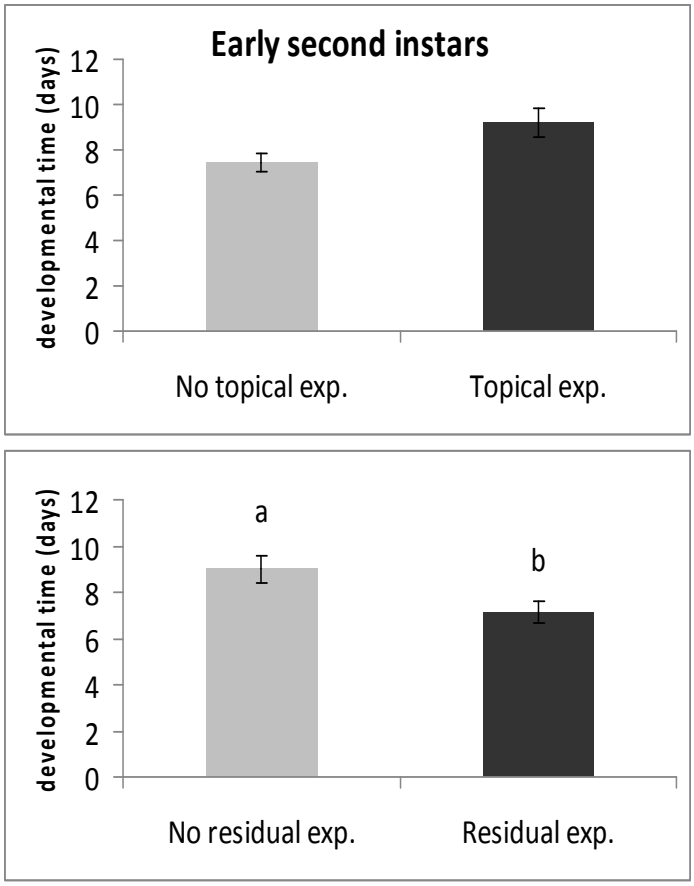

Figure 7 - Developmental times of *F. occidentalis* early second instars to prepupae. Different letters indicate significant differences at t test to the least square means ($\alpha = 0.05$).

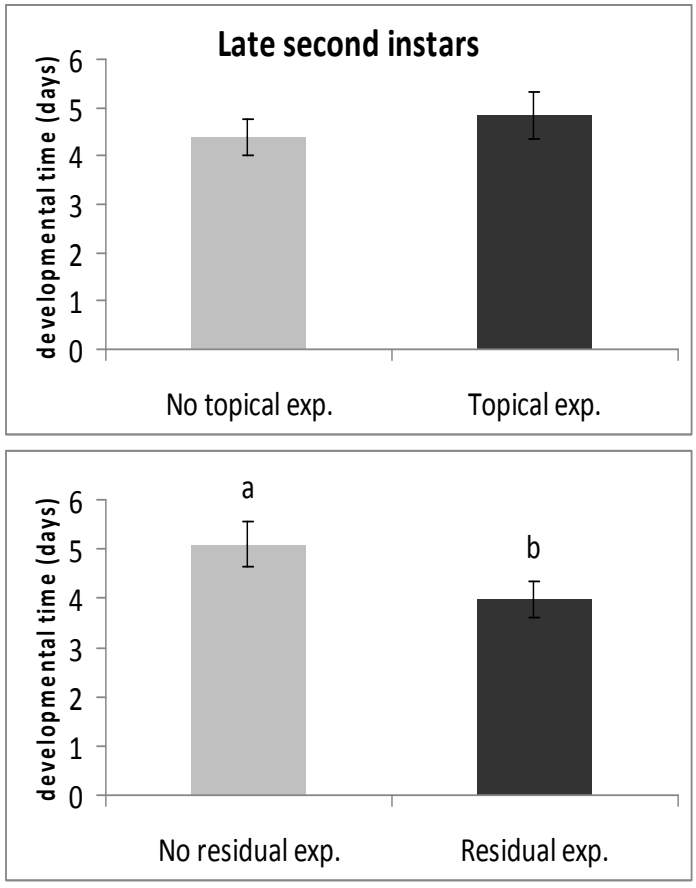

Figure 8 - Developmental times of *F. occidentalis* late second instars to prepupae. Different letters indicate significant differences at t test to the least square means ($\alpha = 0.05$).

Discussion

The efficacy of *B. bassiana* JW-1, ATCC 74040 strain in controlling a number of insect and mite pests has been shown in laboratory and field trials (e.g., Akey and Henneberry, 1998; Duso et *al*., 2008; Ortu et *al*., 2009; Oreste et *al*., 2012). In our study, *B. bassiana* reduced significantly the survival of *F. occidentalis*. These effects increased over the time and varied depending on life stage and the route of exposure to the pathogen.

First instar thrips were significantly affected by *B. bassiana* but the route of exposure was crucial in determining these effects. First instars show a localized feeding behaviour and a low motility that reduce the probability of acquiring conidia dispersed onto the leaf surface. This can explain the low mortality effects associated to residual exposure. The direct contact of *B. bassiana*, as a result of topical application, increased the effects of

pathogen on first instars. The virulence of this *B. bassiana* strain associated with features of first instars' cuticle might provide an explanation of greater susceptibility associated with topical exposure. Differences in *F. occidentalis*'s cuticle among different thrips stages (e.g., hardening) could contribute to explain differences observed in pathogenicity; unfortunately knowledge on this topic is only available for late second instars and adults only (Golebiowski et *al.*, 2007; Golebiowski, pers. comm.). The effect of topical exposure was remarkable nine days after application when most of first instars had moulted into second instars and few of them into prepupae (data not reported). The delayed effect of *B. bassiana* on these life stages was confirmed by data related to the combination of topical and residual exposures. Factors involved in this phenomenon need to be identified.

Moulting and associated changes in insect physiology could affect thrips-*B. bassiana* relationships. Vey and Fargues (1977) studied histological and ultrastructural aspects of *Leptinotarsa decemlineata* L. larvae contaminated with *B. bassiana* before moulting. After moulting some larvae showed healing zones on their integument and, for these larvae death was postponed. In their body cavity the authors observed an encapsulation of fungal elements into haemocytic granulomas. Nevertheless, this process was not fully effective: the encapsulation was only partial, and some encapsulated fungal elements were able to escape from granulomas in a late stage of infection. Authors were led to the conclusion that the combination of the rejection of the contaminated integument during ecdysis together with cellular reactions represented a defence mechanism that determined a delay in pathogen development. Additional mechanisms have been found in *Manduca sexta* L. where protease inhibitors highly specific towards *Metharizium anisopliae* Pr1 protease have been found in moulting fluid; this enzyme plays an important role in the pathogenic process (St. Leger et al., 1988; Samuels and Reynolds, 2000).

It is important to consider that *B. bassiana* late inoculum can be provided through recycling from fungus-killed cadavers (e.g., Luz and Fargues, 1998). Since in our case, cadavers were removed from experimental units, the late inoculum seems to be of minor importance. These findings may contribute to explain the delayed effect of *B. bassiana* on topically exposed first instars. We can suggest that the *B. bassiana* inoculum to first instars of *F. occidentalis* was partially reduced by the moult and this process combined with the immunological and biochemical defences, determined the delay in the fungal lethal effects.

It should be stressed that first instar thrips are considered the most susceptible to pesticides among juveniles and thus they represent a crucial target for control measures. The combined effects of 78% in the final assessment date suggests a role for *B. bassiana* in controlling these pests especially when their population structure is dominated by first instars.

Regarding early second instars, mortality was remarkable six and nine days following residual exposure. However, an additive effect was noticed when topical and residual exposures were combined.

Ugine et *al*. (2005a) reported a high susceptibility of early second instar thrips to another strain of *B. bassiana* (GHA) (compared to adults) without significant differences between residual and topical exposures. Our results confirm that second instar thrips can readily acquire lethal doses of conidia from the surface of treated leaves. This phenomenon is likely related to the higher mobility of these stages compared to first instars and has clear implications for thrips control. Ugine et *al*. (2005a) showed that early second instars exposed to conidia within 24 h of their molt were more susceptible to *B. bassiana* than thrips exposed later. They mentioned higher mortality values compared to those reported in our study that are likely due to different *B. bassiana* strains and/or the adopted methodology. Mortality reached a plateau after few days and no differences were observed among the rates of mortality recorded five days post-treatment.

In contrast, we observed a continuous increase of mortality especially with residual exposure that reached the highest levels nine days after treatment. This may be related to the conidial concentration used. Indeed in another study, using the GHA strain, the lethal time of *F. occidentalis* was shortened by increasing the conidial concentration of the inoculum by a 10x factor from 10^5 to 10^8 conidia/ml (Mukawa et *al*., 2011). Here we treated the thrips with a solution of 3.45 x 10^4 conidia/ml and this is likely to explain the differences in the decay of survival. In bioassays pointed out by Ugine et al. (2005a), two treated leaves were put in contact inducing a high probability of contact of thrips with conidia. This approach probably overestimated the effects of fungal application but created a worst case scenario for thrips. A comparison of the two methodologies should be done for a correct interpretation of differences in strain virulence.

For late second instars, corrected mortality values suggest their higher susceptibility to *B. bassiana* compared to early second instars. This seems to be in contrast with observations made by Ugine et al. (2005a) where aged second instar thrips were less susceptible than recently moulted second-instar thrips. Late second instars are the most motile immature stages making them quite susceptible to be contaminated with conidia present on leaves. In natural conditions, late second instars reach the soil where they moult into prepupae and thus can escape to the effects on most pesticides applied to the canopy.

It is worth noting that in the present study we used the JW-1, ATCC 74040 strain of *B. bassiana*, whereas GHA strain has been used in other laboratory investigations. At our knowledge, no direct comparisons have been performed among different *B. bassiana* strains against *F. occidentalis* in the laboratory, while Jacobson et *al*. (2001) compared the efficacy of the two strains on *F. occidentalis* on greenhouse cucumbers. The GHA strain was associated to a higher control of *F. occidentalis* compared to JW-1, ATCC 74040 strain, but the latter strain was used at lower conidial concentrations. *B. bassiana* strains are characterized by a wide variation in their virulence against insects and they can differ in various traits as mycotoxins' production, host range, response to environmental conditions (e.g., Leland et *al*., 2005; Leland and McGuire, 2006, Castrillo et *al*., 2008; Boomsma et *al*., 2014). Only a direct comparison with the same condition and methodologies can clarify the implications of the differences among *B. bassiana* strains in *F. occidentalis* control.

Adults were very susceptible to *B. bassiana* application. Thrips exposed to conidial deposits were more vulnerable to fungal infection than those topically treated with *B. bassiana*. These effects emerged six and nine days after application confirming a relatively slow effect. A significant interaction between the two rates of exposure was detected in these assessment dates as residual exposure gave similar mortality rates than combined exposures. The major effect of residual exposure is likely due to the mobility of adult stages and these results are consistent with those reported by Ugine et *al*. (2005b). Also, Vestergaard et *al*. (1995) reported a higher susceptibility of adults *F. occidentalis* to *Lecanicillium* (= *Verticillium*) *lecanii* than second instars. Similarly, adults of *Megalurothrips sjostedti* (Thysanoptera: Thripidae) resulted to be more susceptible to infection by topically applied *Metarhizium anisopliae* compared to immature stages (Ekesi and Maniania, 2000).

The greater infectivity of *B. bassiana* towards adult thrips compared to second instars is also due to the fact that the former do not moult and are thus exposed for a longer period of time to conidia (Ugine et *al*., 2005b). Lower susceptibility following topical application can be due to the capacity of adults to remove conidia as described by Ellington (1980). Adults exhibit a grooming behaviour, thereby wings are brushed over the body removing conidia or transferring them from ventral to dorsal surfaces and *viceversa*.

Stage-dependent susceptibility to *B. bassiana* has been reported in other studies. Romaňa and Fargues (1992) showed a different susceptibility among different life stages of the hemipteran *Rhodnius prolixus* exposed to *B. bassiana* direct spraying. The susceptibility of *R. prolixus* increased with age and in particular the first instar nymphs were about 700-fold less susceptible than the two oldest stages.

Also, differences in susceptibility to topically applied *B. bassiana* on a phytophagous coleopteran species *Paropis charybdis* in New Zeeland were observed to be depending on insect stages, in which a more rapid and successfully reduction in insect individuals was observed for 1st and 2nd instars when compared to 3rd and 4th instars, whereas adults resulted in relatively low vulnerability to such an entomogenous fungus *B. bassiana* (Hastuti et *al.*, 1999).

Cuticular lipids can reduce the penetration of chemicals, toxins and provide protection from attack by microorganisms and other insects antagonists (Vincent and Wegst, 2004; Ortiz-Urquiza and Keyhani, 2013); comparative analysis among species and life stages within a species can support experimental hypothesis on their susceptibility towards control agents (e.g., Golebiowski et *al*., 2011).

In this framework, the cuticular lipid composition of *F. occidentalis* was analyzed to investigate on its response to fungal pathogens (Golebiowski et *al.* 2007). Cuticular lipids of adult and second instars consisted of two groups of compounds - hydrocarbons and free fatty acids. Adults and second instar cuticle showed the same hydrocarbon pattern, with the exception of n-hentriacontane, detected in adults. However, this difference was not taken into account as regards as its potential role in insect-fungi relationships. A number of saturated and unsaturated fatty acids were identified in the cuticle. Since no potential inhibitors of entomopathogenic fungi were detected in the cuticular lipids of thrips authors stressed about the importance of fungal pathogens in pest control. Unfortunately first

instars, the most susceptible stage in topical trials, were not considered in this study. Some support to the hypothesis that cuticle features can be involved in a different susceptibility among different life stages emerged in studies conducted on whiteflies. James et *al.* (2003), reported that second and third instars nymphs of *Bemisia argentifolii* were more susceptible to *Paecilomyces fumosoroseus* and *Beauveria bassiana* when exposed topically, than fourth instars; cuticular lipids composition (primarily long-chain fatty acids) was determined to account for such a differences in observed mortality.

In our experiment, *B. bassiana* determined sub-lethal effects on thrips development inducing a faster development of second instars exposed to conidia deposits on leaves. Several publications have suggested the potential role of moulting process in reducing entomopathogenic fungi inoculum in various pest species (e.g., Chandler et *al*., 1993; Vanderberg et *al*., 1998; Ugine et *al*., 2005b; Kim and Robert, 2012 and others cited before). Moulting process can reduce the potential of fungal infection: when insects lose their cuticle many germinated and ungerminated conidia can be lost with it (Vey and Farguez, 1977; Fernandez et *al*., 2001; Ortiz-Urquiza and Keyhani, 2013) and this phenomenon has been observed also in *F. occidentalis* larvae infected by *M. anisopliae* (Vestergaard et *al*., 1995, 1998). The earlier moulting observed here may be linked to the activation of immune defence induced by a sub-lethal exposure to pathogens. Roth and Kurtz (2008) found an accelerated development of *Tribolium castaneum* exposed to *Bacillus thuringiensis*. *Culex pipiens* larvae pupated earlier in response to the infection of the microsporidian *Vavraia culicis* (Agnew et *al*., 1999). As mentioned before, moulting has been associated with the production of a fungal proteinase inhibitor that has been found together with other proteinase inhibitors probably involved in the regulation of the endogenous cuticle-degrading proteinase MFP-1 (Samuels and Reynolds, 2000). In *Bombix mori* L. the expression of a fungal proteinase inhibitor was induced by recombinant baculovirus infection with an inhibition of larval development (Pham et al., 1996). Cuticle represent the first line of defence in arthropods against pathogens and constitute a physical and chemical barrier (Hayek & St. Leger, 1994). Among other arthropods, in American lobster *Homarus americanus* (Milne-Edwards) (Crustacea), Laufer et *al*. (2005) observed as sub-lethal response to shell disease, an induced increase of systemic levels of ecdysone in the haemolymph. The authors argued that this is possibly to constitute a defensive

measure that protect the animal from the effects of the shell disease inducing moulting. From our experiments we were not able to fully understand if moulting is more a collateral consequences of induced defence mechanisms or represents itself a step in the defence process against pathogens. The role of moulting in insect-entomopathogen interactions needs to be clarified and furthers studies are needed to understand the mechanisms behind.

This study has improved the understanding of relative susceptibility of each thrips developmental stage to *B. bassiana* (strain ATCC74040) inoculum, stressing on route of exposure, as key factor in *B. bassiana* infection. Differences in mortality amongst thrips life stages as a function of routes of exposure should be considered to improve the contribute of this entomopathogen fungus in IPM strategies. Differences in susceptibility to *B. bassiana* among thrips life stages related to exposure levels might also provide information on infection dynamics that can occur in field conditions. Additionally, we also found sub-lethal effect induced by the exposure to *B. bassiana* that had never found before.

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Conclusions

In this study we investigated: 1) the spatial-temporal distribution patterns of herbivore thrips (*Frankliniella occidentalis* and *Thrips tabaci*) and their natural enemies (*Aeolothrips* spp. and *Orius* spp.) in a number of greenhouses and their surroundings; 2) the role of the greenhouses' opening on the colonization by pest thrips and their naturally-occurring antagonists; 3) the potential role of some biocontrol agents of *Frankliniella occidentalis* in controlled conditions; 4) the impact of *Beauveria bassiana* on *F. occidentalis* as a function of the routes of exposure.

The analysis of spatial-temporal distribution of phytophagous thrips and their natural enemies evidenced different patterns in arthropod distribution among different greenhouses and their surroundings. *F. occidentalis* populations tended to aggregate inside greenhouses coming from contiguous cultivated or logistic areas. The incidence of flowering plants seems to be a major factor enhancing *F. occidentalis* population increase. The colonization of ornamental plots by *F. occidentalis* was poorly affected by the uncultivated vegetation growing at their margins. Patterns in the colonization of cultivated plots by *T. tabaci* were different from those reported for *F. occidentalis*. The former species was frequently found in the hedgerows and the orchard located at the margins of greenhouses, even in spring. The dynamics of hotspots outside and inside cultivation plots and evidence from traps near the roof strongly suggest a role of the natural or cultivated vegetation in *T. tabaci* colonization of contiguous greenhouses.

Vegetation surrounding greenhouses can affect the colonization of protected crops by predaceous thrips (*Aeolothrips* spp.). Populations of the latter were found to be aggregated inside and outside greenhouses. In contrast, *Orius* spp. populations were detected especially in greenhouse surroundings or in the open field nursery.

The management of areas that are at higher risk of *F. occidentalis* establishment, and the use of thrips-proof screening for preventing *T. tabaci* inflows should be considered in IPM tactics. On the other hand relatively closed compartments were related to a low incidence of associations between herbivore thrips and their antagonists. Reducing barriers around cultivated plots enhanced the colonization by predators (especially by *Orius* spp.), even if pesticides could alter this dynamics. At the same time, these associations established more frequently outside cultivated plots with the decrease in greenhouse opening. Therefore, the influence of greenhouse lateral openings on thrips pest management requires further

investigations.

Studies on biological control of *F. occidentalis* showed the possibility to combine different BCAs acting at canopy or soil level in thrips control on cyclamen. At the same time, we showed that *B. bassiana* can exert a significant impact on thrips survival depending on routes of exposure. These results highlight the possibility to use alternatives to pesticides in thrips control on ornamental crops as recommended by current EU rules.

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