B A S E

Macrolophus pygmaeus (Rambur) as an efficient predator of the tomato leafminer *Tuta absoluta* (Meyrick) in Europe. A review

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The tomato leafminer, *Tuta absoluta* (Meyrick), originates from South America, and remains one of the main tomato pests in this continent. Since its introduction to Europe in 2006, Mediterranean countries have also been exposed to this pest. Because of the endophytic habits of the larvae and ability of adults to reproduce parthenogenetically, chemicals and sexual pheromonebased control methods generate poor results. Recently, the use of biocontrol agents, such as *Macrolophus pygmaeus* Rambur (Heteroptera: Miridae), has been investigated as an alternative means of control, the results of which are presented in this review. *Macrolophus pygmaeus* is a mirid bug that is widely used to control different phytophagous insects in integrated pest management strategies through Europe. Several studies have confirmed the high predation potential of *M. pygmaeus* on *T. absoluta* under laboratory and semi-field conditions. This predator spontaneously colonizes tomato greenhouses in the southern Mediterranean countries. The use of banker plants (*i.e.*, plants that provide a habitat to the predator) improves the colonization ability of this natural enemy. Hence, if the local population size is low, an augmentative strategy could be adopted. Predators may be released before or after the onset of pest infestation, with recommendations varying depending on natural population densities of both the pest and predator. The efficiency of *M. pygmaeus* has also been evaluated when used in combination with other biocontrol agents or with chemicals. This work presents an overview of different types of control strategies using *M. pygmaeus* against the tomato leafminer, *T. absoluta*.

Keywords. Gelechiidae, Macrolophus, biological control, integrated pest management, predatory insects, greenhouses.

Macrolophus pygmaeus (Rambur), prédateur efficace de la mineuse de la tomate Tuta absoluta (Meyrick) en Europe (synthèse bibliographique). La mineuse de la tomate, Tuta absoluta (Meyrick), est considérée comme l'un des principaux insectes ravageurs des cultures de tomates en Amérique du Sud, d'où elle est originaire. Depuis son introduction sur le continent européen en 2006, les pays méditerranéens doivent également faire face aux infestations de ce nouveau ravageur. À cause du caractère endophyte des larves et de leur capacité à se reproduire par parthénogénèse, les méthodes de lutte chimiques et sémiochimiques ne sont pas totalement efficaces. L'utilisation d'insectes auxiliaires, tels que Macrolophus pygmaeus Rambur (Heteroptera : Miridae) représente une alternative explorée récemment et dont les résultats sont rassemblés dans cette synthèse bibliographique. En effet, M. pygmaeus est un prédateur de T. absoluta couramment utilisé dans les programmes de lutte contre plusieurs insectes phytophages. Les différentes études de laboratoire et de terrain qui lui sont dévolues reconnaissent toutes le grand potentiel de M. pygmaeus dans la lutte contre T. absoluta. Le prédateur est natif de la région paléarctique et colonise spontanément les serres de tomates de la région méditerranéenne. Des méthodes dites de conservation visent à améliorer la colonisation naturelle des prédateurs à l'aide de plantes refuges (i.e. plantes qui fournissent un habitat au prédateur). Quand la conservation n'est pas suffisamment efficace, des lâchers de prédateurs peuvent être effectués pour augmenter la population locale. Les lâchers se font soit en prévision des infestations ou en applications curatives. Les recommandations varient en fonction des densités de prédateurs et de ravageurs. Dans le but d'améliorer les résultats de la lutte biologique, il est possible de combiner M. pygmaeus avec d'autres moyens de lutte, que ce soit d'autres prédateurs ou parasitoides, ou des méthodes chimiques. L'ensemble des approches visant la lutte biologique contre T. absoluta à l'aide de M. pygmeus est présenté ici. Mots-clés. Gelechiidae, Macrolophus, contrôle biologique, gestion intégrée des ravageurs, insecte prédateur, serre.

1. INTRODUCTION

The tomato leafminer moth, *Tuta absoluta* (Meyrick) [Lepidoptera: Gelechiidae], is currently considered as a serious agricultural threat to European tomato crops, causing losses of 80% to 100% in areas without control measures (Desneux et al., 2010; Desneux et al., 2011a). The pest pressure varies among the European countries, being higher in the Eastern Mediterranean countries while it has declined to medium levels in Western Mediterranean countries. In Northern European countries, infestations are limited to glasshouses (EPPO, 2011). This moth is 6-7 mm in length, and is native to South America, but was introduced to Spain in 2006. It has a reproduction rate of 10 to 12 generations a year under greenhouse conditions, facilitating the fast invasion of new territories (Desneux et al., 2010). The larvae of this moth preferentially develop on tomato plants (Solanum lycopersicum L.) (Desneux et al., 2010); however, larvae and adults may also feed and reproduce on a wide range of solanaceous plants (Caparros Megido et al., 2013a) and other plants such as cape gooseberry (Physalis peruviana L.), bean (Phaseolus vulgaris L.) and Malva sp. (Tropea Garzia et al., 2012). Immediately after egg hatching, the larvae consume the leaves and fruits creating galleries through the mesophyll layer, reducing the ability of plants to photosynthesize, which hinders plant development. These galleries also allow the entry of a diverse array of pathogens (Urbaneja et al., 2009; Desneux et al., 2010). The most common control method of this pest is the use of insecticides, such as abamectin, spinosad, tebufenozide, and chlorfenapyr (Lietti et al., 2005), and sex pheromones (Caparros Megido et al., 2013b). However, both control strategies generate poor or non lasting results (Michereff Filho et al., 2000; Hassan et al., 2009; Vacas et al., 2011). For instance, the efficacy of the sex pheromone strategies is negatively affected by the ability of T. absoluta females to reproduce parthenogenetically (Caparros Megido et al., 2012), while the endophytic (i.e., ability to live within the plant) nature of the larvae reduces the effectiveness of insecticides (Lietti et al., 2005). Moreover, the larvae quickly develop resistance to insecticides (Guedes et al., 2012). Consequently, other strategies are being investigated such as the use of entomopathogenetic nematodes (Batalla-Carrera et al., 2010), Bacillus thuringiensis Berliner (González-Cabrera et al., 2010) or sterile male techniques (Cagnotti et al., 2012). Among those strategies under evaluation, a promising alternative form of pest management is the use of biocontrol agents (Desneux et al., 2011b; Cabello et al., 2012; Zappalà et al., 2013).

Macrolophus pygmaeus Rambur (Heteroptera: Miridae) is a mirid bug that occurs in the Palaeartic region (Sanchez et al., 2012), and is considered as a

principal natural enemy of tomato pests in this region (Perdikis et al., 2011). This bug is a highly polyphagous predator, and is already used as a biocontrol agent against various phytophagous insect pests under greenhouse conditions (Nannini et al., 2012). Both nymphs and adults have piercing-sucking mouthparts, and feed on whitefly eggs, aphids, mites, thrips, and moth eggs (Albajes et al., 2002; Perdikis et al., 2008).

The taxonomy of some Macrolophus spp. has been discordant and very dynamic. Macrolophus pygmaeus and Macrolophus melanotoma (Costa) are sympatric species and cryptic owing to their very similar morphology. These two species differ mainly for few and variable features, such as the lateral band behind the eye and differ in the color pattern of the first antennal segment, being white and black in M. melanotoma and entirely black in M. pygmaeus (Castañé et al., 2013). Moreover, according to the synonimization by Carapezza (1995), M. melanotoma was often quoted its synonym M. caliginosus (Wagner). To clarify the situation, researchers have developed molecular techniques and resolved this misidentification using an integrative approach such as crossing experiments, multivariate morphometry and mitochondrial DNA analysis (Perdikis et al., 2003; Martinez-Cascales et al., 2006; Machtelinckx et al., 2009; Castañé et al., 2013; Evangelou et al., 2013). It is now an admitted fact that the predators commercially available for biological control are M. pygmaeus (Castañé et al., 2013). In the following studies, data have been obtained for Macrolophus caliginosus, but will be treated in this review as M. pygmaeus: Arnò et al. (2003), Castañé et al. (2004),), Castañé et al. (2007), Malausa et al. (1987), Sampson et al. (1999), Tedeschi et al. (2001) and Van Schelt et al. (1996).

This review summarizes available data about M. pygmaeus in the particular event of T. absoluta biocontrol. The review discusses laboratory and field assay results as well as current information on the relation between the predator and its pest.

An extensive review of the literature has been performed using SCOPUS database, using all keywords associated with the title and abstract, including the biological materials and methods presented in this review.

2. NATURAL OCCURRENCE OF *M. PYGMAEUS* IN OPEN FIELDS AND GREENHOUSE COLONIZATION

Macrolophus pygmaeus is native to the Paleartic ecozone. It is distributed from Finland to Algeria, the Azores Islands, and Tajikistan (Sanchez et al., 2012). In Spain, *M. pygmaeus* is among the most abundant natural enemies of *T. absoluta* (Arnó et al.,

2009). During the winter, *M. pygmaeus* is found inhabiting potato crops and non-agricultural plants, such as *Dittrichia viscosa* (L.) Greuter, *Cistus* spp., and *Parietaria officinalis* L.; however, in spring the bug moves from these species to colonize agricultural crops (Gabarra et al., 2004). In southern Greece, *M. pygmaeus* occurs from early summer to late autumn in the fields (Lykouressis et al., 2008).

Macrolophus pygmaeus is considered as a natural enemy of *T. absoluta* in southern France, where it was the most abundant predator on tomato (Biondi et al., 2013), Algeria (Guenaoui et al., 2011), Iran (Baniameri et al., 2011) and Spain (Urbaneja et al., 2012).

Greenhouses in the Mediterranean region (southern Palearctic ecozone) are generally made of plastic, with roll-up sides for ventilation, which allows the exchange of insects with the outside environment. Insects tend to colonize greenhouses at the end of spring in western Mediterranean countries, where insecticides are not applied. In Spain, Castañé et al. (2004) monitored insect infestations in 14 greenhouses, and found that at the end of the tomato crop period (*i.e.*, the start of July), all plants were colonized by two species of mirid bugs, Dicyphus tamaninii Wagner (Heteroptera: Miridae) and M. pygmaeus. The latter species represented 74% of all inventoried insects. The presence of tomato plants in the greenhouse, or in the general vicinity, led to higher numbers of individuals (Castañé et al., 2004). This phenomenon has also been documented in Italy, Greece, France, and the Canary Islands (Malausa et al., 1987; Perdikis et al., 1996; Tavella et al., 1997; Carnero et al., 2000). However, those investigations were conducted before T. absoluta invasions in this area. The situation might have slightly changed since then.

3. LABORATORY AND FIELD EVIDENCE OF *M. PYGMAEUS* PREYING ON *T. ABSOLUTA*

Several laboratory experiments have been conducted to evaluate the ability of *M. pygmaeus* to prey on T. absoluta. Under laboratory conditions, starved M. pygmaeus preyed on over 30 T. absoluta eggs daily (Urbaneja et al., 2009). The predation rate recorded in this experiment was higher compared to that reported on other lepidopteran prey, such as Helicoverpa armigera Hübner (Lepidoptera: Noctuidae), 20 eggs, probably because of the smaller size of T. absoluta eggs (Urbaneja et al., 2009). Arnó et al. (2009) reported a predation exceeding 100 T. absoluta eggs per M. pygmaeus adult and per day. Chailleux et al. (2013a) also showed the active predation of M. pygmaeus on T. absoluta. Macrolophus pygmaeus shows a type II functional response; namely, the predation rate increases with the offered prey density leveling off to a plateau at higher densities. More *M. pygmaeus* females than males preyed on *T. absoluta*, with this difference between the sexes becoming stronger with increasing prey density (Urbaneja et al., 2009).

Urbaneja et al. (2009) also investigated under laboratory conditions the predation rate of M. pygmaeus on different T. absoluta instars. Although it is able to feed on all developmental stages, M. pygmaeus preferentially feeds on first instars (Mollá et al., 2009; Urbaneja et al., 2012), with a mean number of two first instar larvae being eaten per day (Urbaneja et al., 2009). Arnò et al. (2003) obtained the same predation rate when *M. pygmaeus* preved on third and second instars of Liriomyza trifolii Burgess (Diptera: Agromyzidae). These larvae are of similar size to the first instar larvae of T. absoluta (Urbaneja et al., 2009). Jaworski et al. (2013) investigated *M. pygmaeus* preference between T. absoluta and Bemisia tabaci Gennadius (Homoptera: Aleyrodidae) using entire tomato plants. The results showed a similar preference between whitefly nymphs and leafminer eggs, but a lower predation rate on leafminer larvae. Adult predators showed a higher predation rate than juveniles. The presence of the leafminers increased adult predation on both pests and decreased juvenile predation. However, these results are obtained by laboratory investigations and may vary under field conditions. Bompard et al. (2013) showed a beneficial effect of *M. pygmaeus* on the tomato leafminer in the greenhouse. The study assessed predator-mediated interactions between two pests, *T. absoluta* and *B. tabaci* in greenhouse, by monitoring the pest and predator populations when released on crops either separately or combined. They showed that the predator significantly reduced both pest populations separately, 30-fold for adult whiteflies and 3.7-fold for the leafminer (Bompard et al., 2013).

4. BIOLOGICAL CONTROL USING *M. PYGMAEUS*

4.1. Conservation: colonization improvement

Conservation biological control consists in habitat manipulation to enhance the action of endemic or exotic natural enemies (Gurr et al., 1999). Usually, predator occurrence is related to the occurrence of target prey. Being zoophytophagous, *M. pygmaeus* offers the advantage of remaining on the crop, even when prey insects are scarce. The plants have a major influence on the survival of *M. pygmaeus* (Ingegno et al., 2011). To effectively establish the population of this predator in the crop, one or several alternative host plants could be planted near the crop requiring protection. These banker plants could also enable the bug population to remain in the vicinity between two crop cycles (Parolin et al., 2012).

Solanum nigrum L. is a major host for M. pygmaeus (Perdikis et al., 2006; Lykouressis et al., 2008; Ingegno et al., 2011). Macrolophus pygmaeus completes its developmental cycle by feeding exclusively on this plant species, although its fecundity is lower than when also feeding on insect prey (Perdikis et al., 2006; Lykouressis et al., 2008). In Crete, M. pygmaeus is also abundant on many non-cultivated plants, including Dimorphotheca aurantiaca DC., Cistus creticus L., Amaranthus blitum L., and Datura stramonium L. (Roditakis et al., 2003). In Italy, large numbers of M. pygmaeus are found on Artemisia vulgaris L. (Ingegno et al., 2009).

Ingegno et al. (2011) investigated the fitness of M. pygmaeus inhabiting different plants, and plant preferences based on olfactometric assays. The plants selected for the study had been previously reported as host plants for Dicyphini, in Piedmont, Italy (Ingegno et al., 2009), and are common in Italy where the experiment was conducted. Capsicum annuum L., Calendula officinalis L. and S. nigrum allowed the predator to survive longer without prey than Salvia officinalis L. and P. officinalis. The predator reached the fourth instar on the first three plants while it died before the second instar on the last two plants. Parietaria officinalis was the least attractive plant to *M. pygmaeus*, but still served as a suitable refuge in the absence of tomato crops (Ingegno et al., 2011). Alomar et al. (2006) reported a high number of predators on C. officinalis in fields confirming the potential of this plant. Hilly landscapes might also favor the entry of this predator into greenhouses (Gabarra et al., 2004).

4.2. Augmentative strategy

Augmentative strategies are based on the release of predators into greenhouses to increase their numbers. This method is widely used for *M. pygmaeus* in the Mediterranean basin. This species has been commercially available since 1994 for use in integrated pest management (IPM) programs, and is being increasingly used in European tomato greenhouses (Castañé et al., 2011). Although M. pygmaeus is a zoophytophagous mirid, it only damages crops at very high population densities and when preys are scarce (Van Schelt et al., 1996; Castañé et al., 2011). Sampson et al. (1999) reported the only case of damages caused by the predator, and highlighted the fact that the number of individuals is a factor influencing the importance of damage. Here, two alternative augmentative strategies are described. The inundative strategy aims to suppress the pest by releasing a large amount of biocontrol agents. The inoculation strategy aims to establish the predator population on the crop before pest infestation. The initial number of predators that are released should be evaluated to reach a sufficient population size before

pest establishment. If the pests begin to damage the plants, more natural enemies must be released within the framework of the second strategy.

Alternative food sources, such as *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) eggs and *Artemia* cysts may be provided to *M. pygmaeus* to accelerate population growth (Perdikis et al., 2008; Put et al., 2012). Indeed, Mollá et al. (2014) proved that the progeny production of the predator feeding on a diet based exclusively on *T. absoluta* and tomato plants in laboratory conditions, was too low to lead to a significant and stable population. Similar observations have been made in the field (Bompard et al., 2013).

A semi-field experiment was conducted in tomato greenhouses, and showed that *M. pygmaeus* inoculation reduced leaflet and fruit infestation of *T. absoluta* by up to 76% and 56%, respectively (Mollá et al., 2009). In Sardinian greenhouses, the weekly application of two *M. pygmaeus* per m² allowed the infesting *T. absoluta* population to be controlled (Nannini et al., 2012). In north-east Spain, where *T. absoluta* causes major damage, one to two *M. pygmaeus* adults per m² are released in greenhouses, when natural predator populations are low (Urbaneja et al., 2012).

Macrolophus pygmaeus may also be released at the early stages of crop growth, even before transplanting the plant crop to the greenhouse (Trottin-Caudal et al., 2012). Adult predators are released on the seedlings, and initially fed with *Ephestia* eggs. The eggs laid by *M. pygmaeus* hatch very soon after transplantation, allowing population growth to start earlier (Trottin-Caudal et al., 2012).

4.3. Integration in IPM schemes

The use of a natural enemy in combination with other biological control agents, predators and parasitoids, or chemical insecticide treatments is also common, and may help attain higher levels of effectiveness.

In Spain, an IPM program based on the combination of M. pygmaeus and Nesidiocoris tenuis Reuter (Heteroptera: Miridae) has been used for many years (Urbaneja et al., 2012). Nesidiocoris tenuis is also a predator of T. absoluta which allows to provide higher leaflet and fruit damage reduction than M. pygmaeus (Mollá et al., 2009), although this predator naturally occurs only in southern countries (Urbaneja et al., 2012). Arnó et al. (2009) evaluated the effectiveness of the IPM program based on the augmentation and conservation of both mirid predators, compared to a conventional plant protection strategy based on insecticide use, in tomato greenhouses and open field. The number of T. absoluta, and the percentage of damaged plants and young fruits were significantly lower in greenhouses and open fields treated with the IPM program. Damage was reduced by 80% on leaves and by 95% on young fruit using the IPM program compared to the conventional strategy (Arnó et al., 2009). The use of two combined predators can lead to intraguild predation (IGP). Indeed, N. tenuis adults may kill juveniles of M. pygmaeus (Perdikis et al., 2014). Moreno-Ripoll et al. (2012) studied the interactions between both predator species under laboratory conditions. Female N. tenuis only showed predation behavior towards M. pygmaeus. When adult females of both predators were exposed to each other without additional prey, progeny of both predators was reduced. Perdikis et al. (2014) studied these interactions on entire plants revealing that M. pygmaeus and *N. tenuis* do not share the same location on the plant. When they are forced to share the same plant material, and in the absence of prey, young M. pygmaeus did not reach the adult stage. Selective insecticides, mainly based on *Bacillus thuringiensis*, were recommended to complement the IPM mirid based program (Urbaneja et al., 2012).

Macrolophus pygmaeus keeps pest numbers below the damage threshold when chemicals are reduced (Perdikis et al., 2011). Arnó et al. (2011) investigated the impact of azadirachtin, spinosad, and indoxacarb on *M. pygmaeus*. Adult female mortality rates were higher with indoxacarb compared to azadirachtin and spinosad. A detrimental effect on the metamorphosis of nymphs was not observed. Nymphs treated with spinosad had fewer offspring as female adults compared to untreated nymphs. No insecticidal effect of spinosad was reported on the adult predator. Azadirachtin causes high mortality to M. pygmaeus in Petri dishes (Tedeschi et al., 2001). However, azadirachtin residues on plants did not affect female adults, or the third or fourth instars. Exposure to azadirachtin in the final days of preimaginal development reduced offspring numbers by 46% (Tedeschi et al., 2001) or 27% (Arnó et al., 2011). In brief, indoxacarb causes mortality, whereas azadirachtin and spinosad reduce offspring numbers through sublethal effects (Biondi et al., 2012; Desneux et al., 2007 for a through review). Azadirachtin and indoxacarb are classified as being slightly harmful to M. pygmaeus according to the International Organisation for Biological Control (IOBC) toxicity classes, whereas spinosad is classified as moderately harmful (Arnó et al., 2011).

Trottin-Caudal et al. (2012) investigated the combination of *M. pygmaeus* and the egg parasitoid *Trichogramma acheae* Nagaraja and Nagarkatti (Hymenoptera: Trichogrammatidae) to control the tomato leafminer, in greenhouses in France. The experiment compared the effectiveness of both biocontrols alone and combined. A density of one adult predator per plant was introduced in the plant nursery 10 days before planting. In addition, two *M. pygmaeus* adults per m² were released in the crop, 8 and 15 days

after planting. The parasitoids were introduced as parasitized *E. kuehniella* eggs at a density of 25 individuals per m² eight times during three months after planting. Plant damage was reduced to a similar extent by each of *M. pygmaeus* and *T. acheae* alone. However, the best protection level was achieved when both agents were released simultaneously (Trottin-Caudal et al., 2012). Similar results were achieved in microcosms assays (Chailleux et al., 2013a) and in greenhouse cages (Chailleux et al., 2013b).

To reach better control levels with two combined biocontrol agents, intraguild predation (IGP) must be avoided. Macrolophus pygmaeus does not attack T. acheae directly but may decrease the control level if IGP occurs on parasitized eggs. Chailleux et al. (2013a) tested the preference of M. pygmaeus between parasitized and unparasitized eggs in no-choice and double-choice assays. Two parasitized egg stages were included in the test, the newly parasitized eggs, which remain yellow, coloured and 4-5 days parasitized eggs which turn to black. In a no choice situation, the predator fed at the same rate on unparasitized and newly parasitized eggs and at a lower rate on old parasitized eggs. In a choice situation, no preference between yellow and unparasitized eggs was observed, but fewer eggs were consumed when black eggs were offered (Chailleux et al., 2013a).

Macrolophus pygmaeus is a valuable agent to control T. absoluta in an IPM program if no broad spectrum insecticides are used (Arnó et al., 2009). Predator releases in nursery plants are the first step to ensure a good establishment of the population (Trottin-Caudal et al., 2012). On the crop, inoculations of 1-2 adults per m² can be applied (Trottin-Caudal et al., 2012; Urbaneja et al., 2012) and the environment can be manipulated to attract predators from outside or make the population build up easier (Perdikis et al., 2011). Also, E. kuehniella eggs can help building up the population faster (Perdikis et al., 2008; Put et al., 2012; Mollá et al., 2014). In southern countries, N. tenuis and T. acheae can be used in combination with *M. pygmaeus* to increase the impact of each agent when used alone (Arnó et al., 2009; Trottin-Caudal et al., 2012; Chailleux et al., 2013a). In northern countries, where temperatures are too low for the development of T. acheae and N. tenuis (Urbaneja et al., 2012), B. thuringiensis based formulations can be reasonably used (González-Cabrera et al., 2010; Urbaneja et al., 2012).

5. PERSPECTIVES

When searching for insect hosts or prey, predators and parasitoids have been shown to rely on host plant and prey related odorant cues. The use of these semiochemicals in pest management is a rapidly growing field of research (Arab et al., 2007; Moayeri et al., 2007). Macrolophus pygmaeus has been shown to be attracted to herbivore induced volatiles (HIPVs) emitted by sweet pepper (C. annuum) that had been infested by two pests Tetranychus urticae Koch (Acari: Tetranychidae) and Myzus persicae Sulzer (Homoptera: Aphididae) (Moayeri et al., 2007). Macrolophus *pygmaeus* is also attracted to tomato plants infested by whiteflies, whereas whiteflies alone do not attract the predator (Ingegno et al., 2011). At present, the attraction of this predator by HIPVs induced by T. absoluta has not been investigated. If the compounds responsible for the attraction of *M. pygmaeus* could be identified, they could be incorporated into integrated biocontrol strategies focusing at attracting the predators from natural populations occurring outside the greenhouses, guiding them into the greenhouses to infestation hotspots.

Bibliography

- Albajes R. & Alomar O., 2002. Current and potential use of polyphagous predators. *In*: Albajes R., Lodovica Gullino M., Van Lenterer J.C. & Elad Y., eds. *Integrated pest and disease management in greenhouse crops*. Dordrecht, The Netherlands: Kluwer Academic Publishers, 265-275.
- Alomar O., Gabarra R., González O. & Arnó J., 2006. Selection of insectary plants for ecological infrastructure in Mediterranean vegetable crops. *IOBC/WPRS Bull.*, 29(6), 5-8.
- Arab A. et al., 2007. Differential attractiveness of potato tuber volatiles to *Phthorimaea operculella* (Gelechiidae) and the predator *Orius insidiosus* (Anthocoridae). *J. Chem. Ecol.*, **33**(10), 1845-1855.
- Arnò J., Alonso E. & Gabarra R., 2003. Role of the parasitoid Diglyphus isaea (Walker) and the predator Macrolophus caliginosus (Wagner) in the control of leafminers. IOBC/ WPRS Bull., 26, 79-84.
- Arnó J. et al., 2009. *Tuta absoluta*, a new pest in IPM tomatoes in the northeast of Spain. *IOBC/WPRS Bull.*, 49, 203-208.
- Arnó J. & Gabarra R., 2011. Side effects of selected insecticides on the *Tuta absoluta* (Lepidoptera: Gelechiidae) predators *Macrolophus pygmaeus* and *Nesidiocoris tenuis* (Hemiptera: Miridae). J. Pest Sci., 84(4), 513-520.
- Baniameri V. & Cheraghian A., 2011. First report of *Tuta absoluta* in Iran and initial control strategies. In: Proceedings of the EPPO/IOBC/FAO/NEPPO Joint International Symposium on management of Tuta absoluta, November 16-18, 2011, Agadir, Morocco.
- Batalla-Carrera L., Morton A. & García-del-Pino F., 2010. Efficacy of entomopathogenic nematodes against the tomato leafminer, *Tuta absoluta*, in laboratory and greenhouse conditions. *BioControl*, 55(4), 523-530.

- Biondi A. et al., 2012. The non-target impact of spinosyns on beneficial arthropods. *Pest Manage. Sci.*, 68(12), 1523-1536.
- Biondi A. et al., 2013. Indigenous natural enemies attacking *Tuta absoluta* (Lepidoptera: Gelechiidae) in Southern France. *Egypt. J. Biol. Pest Control.*, 23(1), 117-121.
- Bompard A., Jaworski C.C., Bearez P. & Desneux N., 2013. Sharing a predator: can an invasive alien pest affect the predation on a local pest? *Popul. Ecol.*, 55(3), 433-440.
- Cabello T. et al., 2012. Biological control strategies for the south American tomato moth (Lepidoptera: Gelechiidae) in greenhouse tomatoes. J. Econ. Entomol., 105(6), 2085-2096.
- Cagnotti C.L. et al., 2012. Effects of X-rays on *Tuta absoluta* for use in inherited sterility programmes. *J. Pest Sci.*, 85(4), 413-421.
- Caparros Megido R., Haubruge É. & Verheggen F.J., 2012. First evidence of deuterotokous parthenogenesis in the tomato leafminer, *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae). J. Pest Sci., 85(4), 409-412.
- Caparros Megido R., Brostaux Y., Haubruge É. & Verheggen F.J., 2013a. Propensity of the tomato leafminer, *Tuta absoluta* (Lepidoptera: Gelechiidae), to develop on four potato plant varieties. *Am. J. Potato Res.*, **90**(3), 255-260.
- Caparros Megido R., Haubruge É. &Verheggen F.J., 2013b. Pheromone-based management strategies to control the tomato leafminer, *Tuta absoluta* (Lepidoptera: Gelechiidae). A review. *Biotechnol. Agron. Soc. Environ.*, **17**(3), 475-482.
- Carapezza A., 1995. The specific identities of *Macrolophus* melanotoma (A. Costa, 1853) and *Stenodema curticolle* (A. Costa, 1853) (Insecta Heteroptera, Miridae). *Naturalista Siciliano*, **19**, 295-298.
- Carnero A. et al., 2000. Impact of *Nesidiocoris tenuis* Reuter (Hemiptera: Miridae) on whitefly population in protected tomato crops. *IOBC/WPRS Bull.*, **23**(1), 259.
- Castañé C., Alomar O., Goula M. & Gabarra R., 2004. Colonization of tomato greenhouses by the predatory mirid bugs *Macrolophus caliginosus* and *Dicyphus tamaninii*. Biol. Control, **30**(3), 591-597.
- Castañé C., Alomar Ò., Riudavets J. & Gemeno C., 2007. Reproductive biology of the predator *Macrolophus caliginosus*: effect of age on sexual maturation and mating. *Biol. Control*, 43(3), 278-286.
- Castañé C., Arnó J., Gabarra R. & Alomar O., 2011. Plant damage to vegetable crops by zoophytophagous mirid predators. *Biol. Control.*, 59(1), 22-29.
- Castañé C. et al., 2013. Taxonomic identification of Macrolophus pygmaeus and Macrolophus melanotoma based on morphometry and molecular markers. Bull. Entomol. Res., 103(2), 204-215.
- Chailleux A. et al., 2013a. Potential for combined use of parasitoids and generalist predators for biological control of the key invasive tomato pest *Tuta absoluta*. *J. Pest Sci.*, **86**(3), 533-541.

- Chailleux A. et al., 2013b. Suitability of the pest-plant system *Tuta absoluta* (Lepidoptera: Gelechiidae) - tomato for *Trichogramma* (Hymenoptera: Trichogrammatidae) parasitoids and insights for biological control. *J. Econ. Entomol.*, **106**(6), 2310-2321.
- Desneux N., Decourtye A. & Delpuech J.M., 2007. The sublethal effects of pesticides on beneficial arthropods. *Annu. Rev. Entomol.*, **52**, 81-106.
- Desneux N. et al., 2010. Biological invasion of European tomato crops by *Tuta absoluta*: ecology, geographic expansion and prospects for biological control. *J. Pest Sci.*, **83**(3), 197-215.
- Desneux N., Luna M.G., Guillemaud T. & Urbaneja A., 2011a. The invasive South American tomato pinworm, *Tuta absoluta*, continues to spread in Afro-Eurasia and beyond: the new threat to tomato world production. *J. Pest Sci.*, 84(4), 403-408.
- Desneux N. et al., 2011b. Potential for direct interference between natural enemies of *Tuta absoluta* on tomato. *Acta Hortic.*, **917**, 31-37.
- EPPO, 2011. EPPO/IOBC/FAO/NEPPO Joint International Symposium on management of *Tuta absoluta*: summary. *In: Proceedings of the EPPO/IOBC/FAO/NEPPO Joint International Symposium on management of* Tuta absoluta, *November 16-18*, 2011, *Agadir, Morocco*.
- Evangelou V.I. et al., 2013. Discrimination of two natural biocontrol agents in the Mediterranean region based on mitochondrial DNA sequencing data. *Biochem. Genet.*, 51(11-12), 825-840.
- Gabarra R. et al., 2004. Movement of greenhouse whitefly and its predators between in- and outside of Mediterranean greenhouses. *Agric. Ecosyst. Environ.*, **102**(3), 341-348.
- González-Cabrera J., Mollá O., Montón H. & Urbaneja A., 2010. Efficacy of *Bacillus thuringiensis* (Berliner) in controlling the tomato borer, *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae). *BioControl*, **56**(1), 71-80.
- Guedes R.N.C. & Picanço M.C., 2012. The tomato borer *Tuta absoluta* in South America: pest status, management and insecticide resistance. *EPPO Bull.*, **42**(2), 211-216.
- Guenaoui Y., Bensaad R. & Ouezzani K., 2011. Importance of native polyphagous predators able to prey on *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae) on tomato crop. In: Proceedings of the EPPO/IOBC/FAO/NEPPO Joint International Symposium on management of Tuta absoluta, November 16-18, 2011, Agadir, Morocco.
- Gurr G.M. & Wratten S.D., 1999. Integrated biological control: a proposal for enhancing success in biological control. *Int. J. Pest Manage.*, **45**(2), 81-84.
- Hassan M.N. & Alzaïdi S., 2009. *Tuta absoluta* a serious pest advancing in the Mediteranean region. Role of pheromones in management strategies. *Int. Pest Control.*, 51(2), 85-87.
- Ingegno B.L., Pansa M.G. & Tavella L., 2009. Tomato colonization by predatory bug (Heteroptera: Miridae)

in agroecosystems of NW Italy. *IOBC/WPRS Bull.*, 49, 287-291.

- Ingegno B.L., Pansa M.G. & Tavella L., 2011. Plant preference in the zoophytophagous generalist predator *Macrolophus pygmaeus* (Heteroptera: Miridae). *Biol. Control.*, 58(3), 174-181.
- Jaworski C.C. et al., 2013. Preference and prey switching in a generalist predator attacking local and invasive alien pests. *PLoS ONE*, **8**(12), e82231.
- Lietti M.M.M., Botto E. & Alzogaray R.A., 2005. Insecticide resistance in Argentine populations of *Tuta absoluta*. *Neotrop*. *Entomol.*, **34**(1), 113-119.
- Lykouressis D., Giatropoulos A., Perdikis D. & Favas C., 2008. Assessing the suitability of noncultivated plants and associated insect prey as food sources for the omnivorous predator *Macrolophus pygmaeus* (Hemiptera: Miridae). *Biol. Control.*, **44**(2), 142-148.
- Machtelinckx T. et al., 2009. Wolbachia induces strong cytoplasmic incompatibility in the predatory bug *Macrolophus pygmaeus*. *Insect Mol. Biol.*, **18**(3), 373-381.
- Malausa J.C., Drescher J. & Franco E., 1987. Prospectives for the use of the predacious bug *Macrolophus caliginosus* Wagner (Heteroptera: Miridae) on glasshouse crops. *IOBC/WPRS Bull.*, **10**(2), 106-107.
- Martinez-Cascales J.I., Cenis J.L., Cassis G. & Sanchez J.A., 2006. Species identity of *Macrolophus melanotoma* (Costa 1853) and *Macrolophus pygmaeus* (Rambur 1839) (Insecta: Heteroptera: Miridae) based on morphological and molecular data and bionomic implications. *Insect Syst. Evol.*, **37**(4), 385-404.
- Michereff Filho M. et al., 2000. Initial studies of mating disruption of the tomato moth. J. Braz. Chem. Soc., 11(6), 621-628.
- Moayeri H.R.S., Ashouri A., Poll L. & Enkegaard A., 2007. Olfactory response of a predatory mirid to herbivore induced plant volatiles: multiple herbivory *vs* single herbivory. *J. Appl. Entomol.*, **131**(5), 326-332.
- Mollá Ó. et al., 2009. Predation by the mirids *Nesidiocoris tenuis* and *Macrolophus pygmaeus* on the tomato borer *Tuta absoluta. IOBC/WPRS Bull.*, **49**, 203-208.
- Mollá O., Biondi A., Alonso-Valiente M. & Urbaneja A., 2014. A comparative life history study of two mirid bugs preying on *Tuta absoluta* and *Ephestia kuehniella* eggs on tomato crops: implications for biological control. *BioControl*, **59**, 175-183.
- Moreno-Ripoll R., Agustí N., Berruezo R. & Gabarra R., 2012. Conspecific and heterospecific interactions between two omnivorous predators on tomato. *Biol. Control*, **62**(3), 189-196.
- Nannini M. et al., 2012. Use of predatory mirids for control of the tomato borer *Tuta absoluta* (Meyrick) in Sardinian greenhouse tomatoes. *EPPO Bull.*, **42**(2), 255-259.
- Parolin P., Bresch C., Poncet C. & Desneux N., 2012. Functional characteristics of secondary plants for

increased pest management. *Int. J. Pest Manage.*, **58**(4), 369-377.

- Perdikis D. & Lykouressis D., 1996. Aphid populations and their natural enemies on fresh market tomatoes in central Greece. *IOBC/WPRS Bull.*, **19**(11), 33-37.
- Perdikis D. et al., 2003. Discrimination of the closely related biocontrol agents *Macrolophus melanotoma* (Hemiptera: Miridae) and *M. pygmaeus* using mitochondrial DNA analysis. *Bull. Entomol. Res.*, **93**(6), 507-514.
- Perdikis D. et al., 2006. Establishment of a polyphagous mirid predator in the crop: the importance of non-cultivated plants. *IOBC/WPRS Bull.*, **29**(6), 93-96.
- Perdikis D., Kapaxidi E. & Papadoulis G., 2008. Biological control of insect and mite pests in greenhouse solanaceous crops. *Eur. J. Plant Sci. Biotechnol.*, **2**(1), 125-144.
- Perdikis D., Fantinou A. & Lykouressis D., 2011. Enhancing pest control in annual crops by conservation of predatory Heteroptera. *Biol. Control*, **59**(1), 13-21.
- Perdikis D. et al., 2014. Intraguild predation and sublethal interactions between two zoophytophagous mirids, *Macrolophus pygmaeus* and *Nesidiocoris tenuis*. *Biol. Control*, **70**, 35-41.
- Put K., Bollens T., Wäckers F.L. & Pekas A., 2012. Type and spatial distribution of food supplements impact population development and dispersal of the omnivore predator *Macrolophus pygmaeus* (Rambur) (Hemiptera: Miridae). *Biol. Control*, 63(2), 172-180.
- Roditakis N.E. et al., 2003. Beneficial Hemiptera Anthocoridae and Miridae in Crete. In: Proceedings of the 10th Panhellenic Entomological Congress, November 4-7, 2003, Heraklion, Crete. Book of Abstracts 93.
- Sampson C. & Jacobson R.J., 1999. Macrolophus caliginosus Wagner (Heteroptera: Miridae) a predator causing damage to UK tomatoes. IOBC/WPRS Bull., 22(1), 213-216.
- Sanchez J.A., Spina M.L. & Perera O.P., 2012. Analysis of the population structure of *Macrolophus pygmaeus* (Rambur) (Hemiptera: Miridae) in the Palaearctic region using microsatellite markers. *Ecol. Evol.*, 2(12), 3145-3159.

- Tavella L., Alma A. & Sargiotto C., 1997. Samplings of Miridae Dicyphinae in tomato crops of Northwest Italy. *IOBC/WPRS Bull.*, 20(4), 249-256.
- Tedeschi R., Alma A. & Tavella L., 2001. Side-effects of three neem (*Azadirachta indica* A. Juss) products on the predator *Macrolophus caliginosus* Wagner (Het., Miridae). J. Appl. Entomol., **125**(7), 397-402.
- Tropea Garzia G., Siscaro G., Biondi A. & Zappalà L., 2012. *Tuta absoluta*, a South American pest of tomato now in the EPPO region: biology, distribution and damage. *EPPO Bull.*, 42(2), 205-210.
- Trottin-Caudal Y., Baffert V., Leyre J.M. & Hulas N., 2012. Experimental studies on *Tuta absoluta* (Meyrick) in protected tomato crops in France: biological control and integrated crop protection. *EPPO Bull.*, 42(2), 234-240.
- Urbaneja A., Montón H. & Mollá O., 2009. Suitability of the tomato borer *Tuta absoluta* as prey for *Macrolophus pygmaeus* and *Nesidiocoris tenuis*. J. Appl. Entomol., 133(4), 292-296.
- Urbaneja A., Gonzalez-Cabrera J., Arno J. & Gabarra R., 2012. Prospects for the biological control of *Tuta absoluta* in tomatoes of the Mediterranean basin. *Pest Manage. Sci.*, **68**(9), 1215-1222.
- Vacas S., Alfaro C., Primo J. & Navarro-Llopis V., 2011. Studies on the development of a mating disruption system to control the tomato leafminer, *Tuta absoluta* Povolny (Lepidoptera: Gelechiidae). *Pest Manage. Sci.*, 67(11), 1473-1480.
- Van Schelt J., Klapwijk J., Letard M. & Aucouturier C., 1996. The use of *Macrolophus caliginosus* as a whitefly predator in protected crops. *In*: Gerling D. & Mayer R.T. *Bemisia*, 1995: taxonomy, biology, damage, control and management. Andover, UK: Intercept.
- Zappalà L. et al., 2013. Natural enemies of the South American moth, *Tuta absoluta*, in Europe, North Africa and Middle East, and their potential use in pest control strategies. J. Pest Sci., 86(4), 635-647.

(70 ref.)